CALIFORNIA SPOTTED OWL POPULATION DYNAMICS IN THE CENTRAL SIERRA NEVADA: AN ASSESSMENT USING MULTIPLE TYPES OF DATA

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Abstract. The California spotted owl (*Strix occidentalis occidentalis*) is a focal management species in the Sierra Nevada because it uses late-seral forests for roosting and nesting. Thus, obtaining accurate and precise estimates of population trends is necessary to reliably assess the effects of management actions and habitat change on this species. To demonstrate how this objective can be better met, I used multiple data types from a long-term population study in the central Sierra Nevada, as opposed to the typical approach of using only mark-recapture data. First, I compared population trends estimated from occupancy and mark-recapture data. Occupancy surveys are more cost-effective than mark-recapture studies for monitoring territorial species over large spatial extents. I found that the realized change in territory occupancy from 1993-2010 (Δ_t = 0.702, 95% CI 0.552–0.852) closely matched the realized population change estimated from mark-recapture data (Δ_t = 0.725, 95% CI 0.445–1.004). This suggested that occupancy can provide reliable inferences on population trends, especially when funds preclude more intensive mark-recapture studies. I recognize, however, that mark-recapture studies provide important demographic information not provided by occupancy studies, which may allow the identification of life-history stages that are limiting a population. Second, I developed an integrated population model (IPM) to obtain estimates of population change for my study population from 1990-2012 because IPMs may improve the precision of parameter estimates. My IPM incorporated count, reproductive, and mark-recapture data. I observed a significant population decline, as evidenced by the geometric mean of the finite rate of population change ($\widehat{\overline{\lambda t}}$ = 0.969, 95% CRI 0.957, 0.980) and the resulting realized population change (proportion of the initial

population present in 2012; $\hat{\Delta}_{2012}$ = 0.501, 95% CRI 0.383, 0.641). My IPM provided more precise estimates of realized population change than either the occupancy or mark-recapture analyses, but I did not account for covariance among the demographic rates in my IPM, which may have resulted in "false" precision (i.e., underestimation of the true variance). If covariances are incorporated into the IPM, they have excellent potential as a tool for assessing the status of species of conservation or management concern. My results also suggested that continued monitoring of this population and reconsideration of the California spotted owl's status under the U. S. Endangered Species Act may be warranted.

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THE RELATIONSHIP BETWEEN OCCUPANCY AND ABUNDANCE IN A CALIFORNIA SPOTTED OWL POPULATION

Land and resource managers often use detection-nondetection surveys to monitor the populations of species that may be affected by factors such as habitat alteration, climate change, and biological invasions. Relative to mark-recapture studies, using detection-nondetection surveys is more cost-effective, and recent advances in statistical analyses allow the incorporation of detection probability, covariates, and multiple seasons. I examined the efficacy of using detection-nondetection data (relative to mark-recapture data) for monitoring population trends of a territorial species, the California spotted owl (*Strix occidentalis occidentalis*). I estimated and compared the finite annual rates of population change (λ_t) and the resulting realized population change (Δ_t) from both occupancy and mark-recapture data collected over 18 years (1993-2010). I used multiseason, robust-design occupancy models to estimate that territory occupancy declined during the study (Δ_t = 0.702, 95% CI 0.552–0.852) due to increasing territory extinction rates ($\hat{\varepsilon}_{1993}$= 0.019 [SE 0.012]; $\hat{\varepsilon}_{2009}$= 0.134 [SE 0.043]) and decreasing colonization rates ($\hat{\gamma}_{1993}$= 0.323 [SE 0.124]; $\hat{\gamma}_{2009}$= 0.242 [SE 0.058]). I used Pradel's temporal-symmetry model for mark-recapture data to estimate that the population trajectory closely matched the trends in territory occupancy (Δ_t = 0.725, 95% CI 0.445–1.004). Individual survival was constant during the study ($\hat{\varphi}_{1993}$= 0.816 [SE 0.020];

$\hat{\varphi}_{2009}$= 0.815 [SE 0.019]), whereas recruitment declined slightly ($\hat{f}_{1993}$= 0.195 [SE 0.032]; $\hat{f}_{2009}$= 0.160 [SE 0.023]). Thus, I concluded that detection-nondetection data can provide reliable inferences on population trends, especially when funds preclude more intensive mark-recapture studies.

INTRODUCTION

A primary responsibility of land and resource managers is to monitor (often over large spatial scales) the population trends of focal species that may be affected by changing future conditions, such as habitat change, climate change, and biological invasions. The use of detection-nondetection data (i.e., occupancy monitoring) may be a cost-effective, robust means of achieving this goal (Noon et al. 2012). Furthermore, recent advances in the statistical analyses of site-occupancy data allow the incorporation of imperfect detection, site- and survey-specific covariates, multiseason dynamics, and multiple states to assess a wide range of ecological and management questions, which enhances the utility of occupancy analyses (MacKenzie et al. 2006; Nichols et al. 2007).

Mark-recapture studies offer an alternative means of monitoring populations and provide more detailed data on demographic vital rates, such as survival and recruitment (Armstrup et al. 2005). However, mark-recapture studies are labor intensive, relatively costly, and generally encompass a small geographic area due to these constraints. In contrast, occupancy studies require surveying for only the presence or absence of a species and generally allow a larger area to be surveyed at a lower cost (Noon et al.

2012). Furthermore, metapopulation models and species-abundance distributions describe a fundamental, theoretical relation between occupancy and abundance so that site occupancy should provide a useful index for population status (Royle et al. 2005; Borregaard & Rahbek 2010). The results of some empirical research support the theoretical relation between occupancy and abundance. For example, Zuckerberg et al. (2009) found strong correlations between regional occupancy and relative abundance for a wide range of bird species in New York State over 2 periods. For these reasons, researchers have recently used detection-nondetection data, rather than mark-recapture data, to monitor the population status of species over large spatial extents (e.g., Burton et al. 2011; Karanth et al. 2011; Thorn et al. 2011). However, I was unaware of existing studies in which annual trends in site occupancy were compared with annual population trends (estimated with mark-recapture data from the same study population), a comparison that would more convincingly demonstrate a close relationship between occupancy and abundance.

The California spotted owl (*Strix occidentalis occidentalis*) is a focal management species in the Sierra Nevada because it uses late-seral forests for nesting and roosting (Gutiérrez et al. 1992). The U.S. Forest Service (USFS) considers the owl a "sensitive" species, which motivated the USFS to develop a Sierra-wide forest management plan (U.S. Forest Service 2004). The owl is highly territorial, displays strong site fidelity, and breeds irregularly, typically producing 1-2 young in years when it reproduces (Gutiérrez et al. 1995). Currently, the USFS monitors owl populations in the Sierra Nevada with long-term, mark-recapture studies designed to detect territorial adults (i.e., those

responding to vocal surveys) (Franklin et al. 2004; Blakesley et al. 2010). The vital rates of those individuals are then quantified annually. These studies require intensive survey effort over large areas because California spotted owls have large home ranges (mean = 555 ha [SE 100] on the basis of data collected within and near our study area) (Williams et al. 2011). Thus, occupancy studies on a regional scale could be an ideal complement to the mark-recapture studies.

To test the efficacy of using occupancy studies to infer population status, I compared long-term trends (1993-2010), estimated from both occupancy and mark-recapture data, in a California spotted owl population in the central Sierra Nevada. I considered each owl territory a site, so the sampling population was similar for both types of data (i.e., all territorial adults on the study area vs. all owl territories). Thus, I expected annual trends in owl site occupancy should be similar to population trends estimated from the mark-recapture data.

STUDY AREA

The study was conducted on a contiguous 35,500-ha area on the Eldorado National Forest in the central Sierra Nevada, California. The Eldorado Density Study Area (EDSA) has been the site of a long-term mark-recapture study of California spotted owls (Seamans et al. 2001; Franklin et al. 2004; Blakesley et al. 2010). The entire area was surveyed each year without regard to land cover, topography, access, or land ownership. Approximately 60% of the EDSA was public land managed by the USFS, and 40% was private land managed by timber companies.

The primary vegetation type on the EDSA was mixed-conifer forest dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). Common understory species included California black oak (*Quercus kelloggii*), bigleaf maple (*Acer macrophyllum*), and tanoak (*Lithocarpus densiflorus*). Red-fir (*A. magnifica*) forest, dominated by red fir and lodgepole pine (*P. contorta*), was present at higher elevations. Other local vegetation types and landscape features included chaparral, black oak woodland, and barren rock. Elevations on the EDSA ranged from 360 to 2400 m, and the climate was characterized by cool, wet winters and warm, dry summers.

METHODS

Spotted Owl Surveys

Surveys were conducted annually for spotted owls from 1986-2010 during the owl breeding season (1 April–31 August). Surveys were not conducted over the entire EDSA in the early years of the study because funding constraints limited the survey effort. Hence, I examined survey coverage of the EDSA (see Survey Coverage of Study Area below) to determine when the survey effort was adequate to include data for analyses. In the surveys spotted owl vocalizations were imitated (vocal lures) for 10 minutes at a survey station or while walking along a survey route. The sex of a responding owl was determined by the pitch of its 4-note territorial call; males have a lower-pitched call than females (Forsman et al. 1984). If owls were detected on

nocturnal surveys, diurnal surveys were conducted to band unmarked owls, resight marked owls, assess reproduction, and band fledglings (Franklin et al. 1996). Owls were banded with a numbered locking metal band on one leg and a unique combination of color band and color tab on the other leg (Franklin et al. 1996). I included both nocturnal and diurnal surveys in my occupancy analyses. I considered a territory to be a site where owls responded to vocal lures and were subsequently observed either roosting or nesting.

Survey Coverage of Study Area

To determine the initial year of complete survey coverage of the EDSA, I used ArcGIS 9.3 (ESRI, Redlands, California) to examine annual survey coverage of the EDSA. I drew a 0.80-km (0.5-mile) circle around each survey point where owls were not detected and a 1.61-km (1-mile) circle around each nest or roost location. I chose the 0.80-km distance because I expected surveyors to be able to hear any owls within this distance that responded during the surveys. I chose the 1.61-km distance because it was unlikely that other territorial owls would occur so close to a given territory (mean nearest-neighbor distance between owl territory centers from 1993-2010 = 2.26 km). I then overlaid these circled areas on a map of the EDSA and calculated the proportion of the EDSA contained within the estimated areas of survey coverage each year. I chose 1993 as the starting year for my analyses because it was the first year that >90% of the EDSA land area was surveyed and ≥90% of the owl territories were surveyed at least once. The surveys conducted prior to 1993 served to develop survey protocols and identify owl territories. My approach was consistent with previous mark-recapture

analyses for the EDSA that did not use data collected prior to 1990 because it was subjectively determined that survey effort was inadequate from 1986-1989 (Franklin et al. 2004; Blakesley et al. 2010).

Occupancy Modeling

I used a multi-season, robust-design occupancy model (MacKenzie et al. 2003) to assess occupancy trends of owls. I divided each breeding season into 10 semimonthly periods (1-15 April, 16-30 April, 1-15 May, 16-31 May, etc.). This approach provided greater biological meaning to the survey occasions at individual territories, relative to sequentially using all surveys conducted at a territory each year. For example, if one territory was first surveyed in early April and another in early June, I believed that it was inappropriate to model the detection probability for the first survey occasion at each site with the same parameter. I chose semimonthly periods to retain as much data as possible without having too many missing observations within a given sampling period. If a territory was not surveyed during a semimonthly period, I treated it as a missing observation. If multiple surveys were conducted within the same period, I assigned a zero to the survey history if no owls were detected during any survey and a one if at least one owl was detected during any survey. The primary sampling periods were breeding seasons (i.e., years), and the secondary sampling periods were the semimonthly periods within each breeding season.

The statistical model contained parameters for initial occupancy (ψ_1), local extinction (ε_t), local colonization (γ_t), and detection probability ($p_{t,j}$) (MacKenzie et al.

2003). I used PRESENCE (version 3.1) (Hines 2006) to compare models with Akaike's information criterion (AIC) (Burnham & Anderson 2002). I used MARK (version 6.1) (White & Burnham 1999) to obtain model-averaged parameter estimates that were based on Akaike weights (ω_i) (Burnham & Anderson 2002). Both programs also provided annual estimates of occupancy ($\hat{\psi}_t$) and rates of change in occupancy ($\hat{\lambda}_t$), which were derived recursively from $\hat{\psi}_1$, $\hat{\varepsilon}_t$, and $\hat{\gamma}_t$ (MacKenzie et al. 2003). I then calculated the geometric mean for the rate of change in occupancy ($\hat{\bar{\lambda}}$) and estimated the realized change in occupancy (Δ_t) as

$$\Delta_t = \prod_{i=1}^{t-1} \hat{\lambda}_i \, . \qquad (1)$$

Thus, Δ_t was the product of $\hat{\lambda}_{1993} \times \hat{\lambda}_{1994} \times \ldots \times \hat{\lambda}_{2009}$ and represented the proportion of the initial population (i.e., the number of occupied territories) remaining in 2010. I obtained variance estimates for $\hat{\bar{\lambda}}$ and Δ_t with the delta method (Powell 2007).

I conducted the modeling in 2 stages. First, I used the fully parameterized model (ψ_1, ε_t, γ_t, $p_{t,j}$) to model within-season *p*. I developed 16 models containing covariates that I hypothesized to affect *p* on survey occasion *j* during year *t* (Table 1). I used month as a covariate because each month corresponded to a different stage of the owl's breeding cycle and breeding-cycle stage affects owl behavior (April, incubation period; May, brooding; June, young fledged from nest; July, fledglings and adults typically near nest tree; August, fledglings and adults typically farther from nest tree) (Gutiérrez et al. 1995). I separated the survey season into prefledging (1 April–31 May) and postfledging (1

June–31 August) periods because owl behavior changes during the fledging period. I included time trends (linear, quadratic, and log linear) because Seamans and Gutiérrez (2007) found that *p* varied in a log-linear trend over the survey season on the EDSA. I specified that *p* was different on survey occasions after the survey when owls were initially detected at a territory because observers intensified their efforts to relocate detected birds to resight or capture birds and assess reproduction (Riddle et al. 2010). Because I expected nesting owls to be more easily detected than non-nesting owls (Nichols et al. 2007; MacKenzie et al. 2009) I used reproductive status as a covariate. Nesting owls may defend their territories more aggressively (i.e., respond more readily to vocal surveys) or spend more time in the territory core area, where most of the survey effort occurred. I did not include any covariates for survey effort because multiple surveys were often conducted within a sampling period at sites where owls were known to be present (i.e., for the demographic study), which created a spurious, positive relation between survey effort and *p*. I also did not include a covariate for survey type because surveys of different types were often conducted within the same period.

In the second modeling stage, I used the best structure for within-season variation in *p* and compared models in which ε_t, γ_t, and p_t varied in 5 ways: constant (.), different in each year (*t*), linear trend (*T*), quadratic trend (*TT*), and log-linear trend (ln*T*). I considered all possible combinations of temporal trends for ε_t, γ_t, and p_t. I did not include additional covariates (e.g., habitat quality within a territory) because my main interest was to obtain the best estimate of temporal trends in occupancy, not to test biological hypotheses related to territory occupancy.

Mark-recapture Modeling

In prior mark-recapture analyses of some of the data, a temporal-symmetry model (Pradel 1996) was used that contained parameters for finite rate of population change (λ_t), annual survival (φ_t), and capture probability (p_t) and treated λ_t as a random effect (Franklin et al. 2004; Blakesley et al. 2010). Blakesley et al. (2010) used mark-recapture data from 1990-2005 on the EDSA, but they omitted the first 2 and last estimates of λ_t, which may have been confounded with p_t when the parameters were modeled with a categorical time covariate (i.e., a different parameter estimate for each year). I used data from only 1993-2010 in my analyses to maintain congruence with my occupancy modeling. My top models did not include any categorical time covariates, so I did not omit any λ_t estimates from my results.

Furthermore, I used a functional form of Pradel's temporal-symmetry model that contained parameters for recruitment (f_t), φ_t, and p_t, and treated all parameters as fixed effects. Although treating $\hat{\lambda}_t$ as a random effect allows the partitioning of process variance (i.e., variation in $\hat{\lambda}_t$ due to covariate effects) from sampling variance (i.e., variation in $\hat{\lambda}_t$ due to random sampling [Burnham & White 2002]), I wished to maintain an approach consistent with my occupancy modeling. An additional benefit of my approach was the explicit modeling of both mechanisms (recruitment and survival) responsible for population change.

I used MARK (version 6.1) to compare competing models with AIC_c and obtain model-averaged parameter estimates on the basis of ω_i. MARK provided annual estimates of finite rates of population change ($\hat{\lambda}_t$), which were derived from $\hat{f}_t$ and $\hat{\varphi}_t$ (Pradel 1996). I then calculated $\bar{\hat{\lambda}}$, Δ_t, and their variances as above (see Occupancy Modeling above).

As with the occupancy modeling, I conducted the mark-recapture modeling in 2 stages. First, I used the fully parameterized model (f_t, φ_t, p_t) to model p_t. In this case, *p* refers to the probability of recapturing a marked individual that was still alive during a given year, whereas *p* in the occupancy modeling referred to the probability of detecting an owl(s) at an occupied territory during a given survey. I developed 12 models containing covariates that I hypothesized could affect *p* (Table 2). Walk-in effort represented the amount of time spent conducting diurnal surveys in a given year. Relatively greater walk-in effort was positively correlated with *p* on the EDSA for survival analyses (Blakesley et al. 2010). Blakesley et al. (2010) also found that a bird's sex was related to *p* on the EDSA. Finally, I included time trends (linear, quadratic, and log linear) because observer proficiency may have improved as the study progressed.

In the second modeling stage, I used the best structure for p_t and compared models in which f_t and φ_t varied temporally in 5 ways: constant (.), different in each year (*t*), linear trend (*T*), quadratic trend (*TT*), and log-linear trend (ln*T*). I considered all possible combinations of temporal trends for f_t and φ_t. As with the occupancy modeling, I did not include additional biological covariates because my goal was to obtain the best

estimate of temporal trends in population size, not to test biological hypotheses related to individual survival or recruitment.

RESULTS

Territory Occupancy

Forty-five owl territories were located from 1993-2010, and owls had been detected at least once at all sites by 1997. Reproduction by owls was observed at 39 of 45 territories at least once during the study, which indicated I had identified biologically relevant territories. At least 1 owl was detected at 40 of 45 (90.0%) territories in 1993, but at only 26 of 45 (57.8%) territories surveyed in 2010. Thus, naïve territory occupancy estimates, which did not account for imperfect detection, indicated occupancy declined by 31% (14/45) during the study.

In the first modeling stage, model $\{\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{ initial + repro}}\}$ had 100.0% of the Akaike weight among the 16 candidate models. Therefore, I used $p_{t,\text{ initial + repro}}$ in all second-stage models, of which $\{\psi_1, \gamma., \varepsilon_{\text{lnT}}, p_{\text{T, initial+repro}}\}$ was the top-ranked model (Table 3). However, considerable uncertainty existed regarding which model best fit the data as the top 7 models were within 2.0 AIC units of each other (Burnham & Anderson, 2002). Parameter estimates from model $\{\psi_1, \gamma., \varepsilon_{\text{lnT}}, p_{\text{T, initial + repro}}\}$ indicated that within-year detection probability of owls was higher on surveys following the initial detection of an owl at a territory ($\hat{\beta}_{\text{initial}}$ = 1.20 [SE 0.11]) and higher for nesting owls ($\hat{\beta}_{\text{repro}}$ = 1.63 [SE

0.14]). Annual detection probabilities were generally high, particularly for nesting owls (Fig. 1).

Due to model-selection uncertainty, I obtained model-averaged estimates for $\hat{\gamma}_t$, $\hat{\varepsilon}_t$, and $\hat{\psi}_t$ with the 21 models that had > 80% of the Akaike weight (Fig. 1). I used the top 80% because all models outside of this set had low support ($\omega_i \leq 0.02$). When a model contained a temporal covariate for either $\hat{\gamma}_t$ or $\hat{\varepsilon}_t$, the indicated trend was always negative for $\hat{\gamma}_t$ and positive for $\hat{\varepsilon}_t$. Thus, territory extinction increased over time ($\hat{\varepsilon}_{1993}$ = 0.019 [SE 0.012]; $\hat{\varepsilon}_{2009}$= 0.134 [SE 0.043]), whereas territory colonization decreased over time ($\hat{\gamma}_{1993}$= 0.323 [SE 0.124]; $\hat{\gamma}_{2009}$= 0.242, SE = 0.058). As a result, territory occupancy declined during the study ($\hat{\psi}_{1993}$ = 0.957 [SE 0.045]; $\hat{\psi}_{2010}$= 0.671 [SE 0.069]). The model-averaged estimates of ψ corresponded well with the naïve estimates of occupancy, despite a decline in the annual estimates of *p* during the study (Fig. 2). The estimated and naïve occupancy estimates did not diverge because *p* remained relatively high throughout the study, and sufficient surveys were conducted at a territory each year (average number of surveys per territory = 3.9) to detect owls reliably.

Mark-recapture Abundance

In the first modeling stage, model $\{\varphi_t, f_t, p_{\text{sex+effort}}\}$ was the top-ranked model and had 35.7% of the Akaike weight among the 12 candidate models, so I used $p_{\text{sex+effort}}$ for detection probability in all second-stage models. In the second modeling stage, model $\{\varphi., f., p_{\text{sex+effort}}\}$ was the top-ranked model (Table 4). Parameter estimates from model

$\{\varphi., f., p_{\text{sex+effort}}\}$ indicated that φ and *f* were constant during the study period and that *p* was higher for male owls ($\hat{\beta}_{\text{sex}}$ = 0.54 [SE 0.25]) and positively correlated with annual walk-in survey effort ($\hat{\beta}_{\text{effort}}$ = 1.46 [SE 0.67]). However, the top 6 models were within 2.0 AIC units of each other.

Due to model-selection uncertainty, I obtained model-averaged estimates of $\hat{\varphi}_t$, $\hat{f}_t$, and $\hat{\lambda}_t$ with the 14 models that had ≥ 95.0% of the Akaike weight (Fig. 3). The top 4 models specified that φ was constant; when a model contained a temporal covariate for $\hat{\varphi}_t$, the trend was weakly negative. The top model specified that *f* was constant; when a model contained a temporal covariate for $\hat{f}_t$, the trend was negative. Thus, survival was nearly constant over time ($\hat{\varphi}_{1993}$= 0.816 [SE = 0.020]; $\hat{\varphi}_{2009}$= 0.815 [SE 0.019]), whereas recruitment decreased slightly ($\hat{f}_{1993}$= 0.195 [SE 0.032]; $\hat{f}_{2009}$= 0.160 [SE 0.023). As a result, the finite rate of population change slightly declined during the study ($\hat{\lambda}_{1993}$ = 1.011 [SE 0.035]; $\hat{\lambda}_{2009}$= 0.975 [SE 0.024]).

Occupancy versus Abundance

The realized change in occupancy (Δ_t = 0.702, 95% CI 0.552–0.852) (Fig. 4) and the geometric mean of annual change in occupancy ($\hat{\bar{\lambda}}$ = 0.979, 95% CI 0.967–0.992) both suggested that territory occupancy declined from 1993-2010. Changes in occupancy within my study area should reflect changes in abundance unless the average number of owls detected at a territory also changed over time (i.e., more or fewer single owls).

Thus, I performed a linear regression of the number of owls detected per territory versus year, and the slope was not significantly different from 0.0 ($\beta = -0.004$, $F_{1,16} = 1.13$, $p = 0.30$).

The realized change in population size ($\Delta_t = 0.725$, 95% CI 0.445–1.004) (Fig. 4) and the geometric mean of the finite rate of population change ($\hat{\hat{\lambda}} = 0.981$, 95% CI 0.959–1.004) also suggested that population size declined from 1993-2010, but the 95% CI slightly overlapped 1.0 for both parameters. The realized change in territory occupancy closely matched the realized population change estimated from mark-recapture data, although the realized population change estimates were less precise (Fig. 4).

DISCUSSION

The realized change in population I estimated on the basis of occupancy closely matched the realized population change estimated from mark-recapture data. This result suggests occupancy monitoring may offer an accurate, cost-effective means to monitor the population trends of territorial species over large spatial extents. The relation between occupancy and abundance may be less strong for nonterritorial species (e.g., semicolonial [Estrada & Arroyo 2012]), so I encourage assessments of the occupancy-abundance relation for such species. Occupancy models that incorporate observed counts of individuals and imperfect detection should be well suited for such applications (Royle et al. 2005).

I obtained more precise parameter estimates with occupancy modeling relative to mark-recapture modeling. The determination of the effective sample size in occupancy

studies has not been fully resolved, but I obtained a larger sample size with the occupancy data because the robust-design occupancy model accommodated multiple surveys (i.e., data points) at a territory each year. Conversely, I used a mark-recapture model that used a single datum each year for the marked individuals in the population. Robust-design models that accommodate missing observations are available for mark-recapture data (Pollock 1982), but I believe a site-based occupancy approach offers greater flexibility. For example, if the entire study area is not surveyed during each secondary sampling period, it is unclear how one would generally determine which individuals were not sampled during that period. Alternatively, the size of the study area can be increased to add more individuals, but this again requires substantial survey effort for species with large home ranges. In contrast, additional sampling units can be more easily added with occupancy surveys because the sampling unit is the site (whether defined as quadrats, territories, etc.), not the individual.

For the occupancy modeling, territory extinction increased over time, and colonization rates were insufficient to maintain occupancy at its initial level. Annual territory extinction was low during the study, but its effects were significant because most territories were occupied at the study's onset and colonization rates were also low. Territories may not have been colonized because habitat alteration during the study (e.g., logging, high-intensity wildfire) may have affected the quality of vacant owl territories (Seamans & Gutiérrez 2007). In addition, the mark-recapture modeling showed a declining trend in individual recruitment, so the population may have produced an

insufficient number of owls to colonize vacant territories and maintain occupancy at its initial level.

I identified 2 factors that greatly affected the detection probability (*p*) in my occupancy analysis. First, *p* increased after the initial detection of owls at a territory during a given year (see Riddle et al. 2010). Owl demographic studies are designed to capture birds (either by banding unmarked birds or resighting marked birds) and to determine reproductive activity (Franklin et al. 1996), so observers intensify their efforts to locate birds after initial detection. This phenomenon suggests that future occupancy analyses for studies originally designed to collect mark-recapture data should include a within-year, initial-detection effect in the model structure. Second, I found that nesting spotted owls were more likely to be detected, which confirmed the results of prior analyses (Nichols et al. 2007; MacKenzie et al. 2009). My results also supported the need to model detection probability appropriately during occupancy analyses to reduce bias in site-occupancy estimates (MacKenzie et al. 2006).

My results suggested that occupancy data can provide reliable information on wildlife population trends, as evidenced by the concurrent declines in territory occupancy and population size of California spotted owls. Therefore, managers may be justified in using less costly, occupancy-based study designs to monitor spotted owls and other species of management concern over large geographic areas. My occupancy models also provided more precise parameter estimates than my mark-recapture models because multiple surveys were conducted at each territory per primary sampling period. A robust-design mark-recapture model could have been used, but it was unclear how one would

determine whether individuals were sampled during a defined secondary sampling period. I caution, however, that occupancy data may be more suitable for inferring the population status of territorial species than those with clumped spatial distributions, unless data collection also includes counts of individual organisms (in addition to the simple detection or non-detection of the target species) and researchers use occupancy models that incorporate such data (Royle et al. 2005).

I encourage future research that incorporates ecological covariates (e.g., habitat quality, habitat change) to elucidate site-occupancy dynamics and inform management decisions that may affect the California spotted owl. For example, managers need information on how timber harvest affects territory extinction and colonization, reproductive output, and individual survival (U.S. Forest Service 2004). I also recognize that mark-recapture studies provide important demographic information not provided by occupancy studies, which may allow the identification of life-history stages that are limiting a population. Thus, the choice of study design will depend on the specific research or management objectives for a given wildlife population.

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Table 1.1. *A priori* models for within-season detection probability (p_j) during occupancy surveys for territorial California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1993-2010.

Model	Description
1) $\psi_1, \gamma_t, \varepsilon_t, p_{t,.}$	Constant on each survey occasion *j*.
2) $\psi_1, \gamma_t, \varepsilon_t, p_{t,j}$	Different on each survey occasion *j*.
3) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{month}}$	Different for each month.
4) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{fledge}}$	Different after young had fledged (June 1).
5) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{T}}$	Varied in a linear time trend.
6) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{TT}}$	Varied in a quadratic time trend.
7) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{lnT}}$	Varied in a log-linear time trend.
8) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{initial}}$	Different after the initial detection at an owl territory.
9) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{repro}}$	Different for nesting owls.
10) $\psi_1, \gamma_t, \varepsilon_t, p_{t,j\,+\,\text{repro}}$	Different on each survey occasion and for nesting owls.
11) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{month}\,+\,\text{repro}}$	Different for each month and for nesting owls.
12) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{fledge}\,+\,\text{repro}}$	Different after young had fledged and for nesting owls.
13) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{T}\,+\,\text{repro}}$	Linear time trend and different for nesting owls.
14) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{lnT}\,+\,\text{repro}}$	Log-linear time trend and different for nesting owls.
15) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{TT}\,+\,\text{repro}}$	Quadratic time trend and different for nesting owls.
16) $\psi_1, \gamma_t, \varepsilon_t, p_{t,\text{initial}\,+\,\text{repro}}$	Different after initial detection and for nesting owls.

Table 1.2. *A priori* models for annual recapture probability (*p*) of marked individual California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1993-2010.

Model	Description
1) $\varphi_t, f_t, p_.$	Constant for all individuals and years.
2) $\varphi_t, f_t, p_{effort}$	Varied by survey effort within each year.
3) φ_t, f_t, p_{sex}	Different for each sex.
4) φ_t, f_t, p_t	Different for each year.
5) $\varphi_t, f_t, p_{sex + effort}$	Different for each sex and varied by annual survey effort.
6) $\varphi_t, f_t, p_{sex + t}$	Different for each sex and year.
7) φ_t, f_t, p_T	Varied in a linear time trend.
8) φ_t, f_t, p_{lnT}	Varied in a log-linear time trend.
9) φ_t, f_t, p_{TT}	Varied in a quadratic time trend.
10 $\varphi_t, f_t, p_{sex + T}$	Linear time trend and different for each sex.
11) $\varphi_t, f_t, p_{sex + lnT}$	Log-linear time trend and different for each sex.
12) $\varphi_t, f_t, p_{sex + TT}$	Quadratic time trend and different for each sex.

Table 1.3. Top-ranked models for multiseason occupancy analysis of California spotted owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1993-2010.

Model[a]	No. parameters	AIC[b]	ΔAIC[c]	ω_i[d]
ψ_1, $\gamma_.$, ε_{lnT}, $p_{T,\ initial+repro}$	8	3081.93	0.00	0.108
ψ_1, $\gamma_.$, ε_T, $p_{T,\ initial+repro}$	8	3082.60	0.67	0.077
ψ_1, $\gamma_.$, ε_{lnT}, $p_{TT,\ initial+repro}$	9	3082.82	0.89	0.069
ψ_1, $\gamma_{lnT.}$, ε_{lnT}, $p_{T,\ initial+repro}$	9	3083.44	1.51	0.051
ψ_1, γ_T, ε_{lnT}, $p_{T,\ initial+repro}$	9	3083.50	1.57	0.049
ψ_1, $\gamma_.$, ε_{TT}, $p_{T,\ initial+repro}$	9	3083.65	1.72	0.046
ψ_1, $\gamma_.$, ε_T, $p_{TT,\ initial+repro}$	9	3083.74	1.81	0.044
ψ_1, γ_{lnT}, ε_T, $p_{T,\ initial+repro}$	9	3084.04	2.11	0.038
ψ_1, γ_T, ε_T, $p_{T,\ initial+repro}$	9	3084.15	2.22	0.036
ψ_1, $\gamma_.$, ε_{TT}, $p_{TT,\ initial+repro}$	10	3084.32	2.39	0.033
ψ_1, γ_{lnT}, ε_{lnT}, $p_{TT,\ initial+repro}$	10	3084.41	2.48	0.031
ψ_1, γ_T, ε_{lnT}, $p_{TT,\ initial+repro}$	10	3084.46	2.53	0.030
ψ_1, γ_{TT}, ε_{lnT}, $p_{T,\ initial+repro}$	10	3084.66	2.73	0.028
ψ_1, $\gamma_.$, ε_T, $p_{t,\ initial+repro}$	24	3085.03	3.10	0.023
ψ_1, $\gamma_.$, ε_{lnT}, $p_{t,\ initial+repro}$	24	3085.05	3.12	0.023
ψ_1, γ_{TT}, ε_T, $p_{T,\ initial+repro}$	10	3085.10	3.17	0.022
ψ_1, γ_{lnT}, ε_{TT}, $p_{T,\ initial+repro}$	10	3085.20	3.27	0.021
ψ_1, γ_{lnT}, ε_T, $p_{TT,\ initial+repro}$	10	3085.25	3.32	0.021

ψ_1, γ_T, ε_{TT}, $p_{T,\ initial+repro}$	10	3085.26	3.33	0.020
ψ_1, γ_T, ε_T, $p_{TT,\ initial+repro}$	10	3085.34	3.41	0.020
ψ_1, γ_{TT}, ε_{lnT}, $p_{TT,\ initial+repro}$	11	3085.62	3.69	0.017

[a] Model variables are defined in Methods.

[b] Akaike's information criterion.

[c] Distance in AIC units from the model with the lowest AIC value.

[d] Akaike weight.

Table 1.4. Top-ranked temporal-symmetry models with recruitment and survival for mark-recapture analysis of a California spotted owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993-2010.

Model[a]	No. parameters	AIC_c[b]	ΔAIC_c[c]	ω_i[d]
$\varphi_{.}, f_{.}, p_{sex+effort}$	5	2326.29	0.00	0.186
$\varphi_{.}, f_{lnT}, p_{sex+effort}$	6	2326.86	0.57	0.139
$\varphi_{.}, f_{T}, p_{sex+effort}$	6	2327.56	1.27	0.099
$\varphi_{.}, f_{TT}, p_{sex+effort}$	7	2327.60	1.31	0.096
$\varphi_{lnT}, f_{.}, p_{sex+effort}$	6	2328.25	1.96	0.070
$\varphi_{T}, f_{.}, p_{sex+effort}$	6	2328.30	2.01	0.068
$\varphi_{T}, f_{lnT}, p_{sex+effort}$	7	2328.88	2.59	0.051
$\varphi_{lnT}, f_{lnT}, p_{sex+effort}$	7	2328.89	2.60	0.051
$\varphi_{T}, f_{T}, p_{sex+effort}$	7	2329.58	3.29	0.036
$\varphi_{lnT}, f_{T}, p_{sex+effort}$	7	2329.59	3.30	0.036
$\varphi_{T}, f_{TT}, p_{sex+effort}$	8	2329.60	3.31	0.035
$\varphi_{lnT}, f_{TT}, p_{sex+effort}$	8	2329.61	3.32	0.035
$\varphi_{TT}, f_{.}, p_{sex+effort}$	7	2330.26	3.97	0.025

[a] Model variables are defined in Methods.

[b] Akaike's Information Criterion adjusted for small sample size.

[c] Distance in AIC_c units from the model with the lowest AIC_c value.

[d] Akaike weight.

Figure 1.1. Estimates of detection probability (SE) at California spotted owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1993-2010, from the top-ranked model (ψ_1, $\gamma.$, ε_{lnT}, $p_{T,\ initial\ +\ repro}$). Note that no birds nested in 2006.

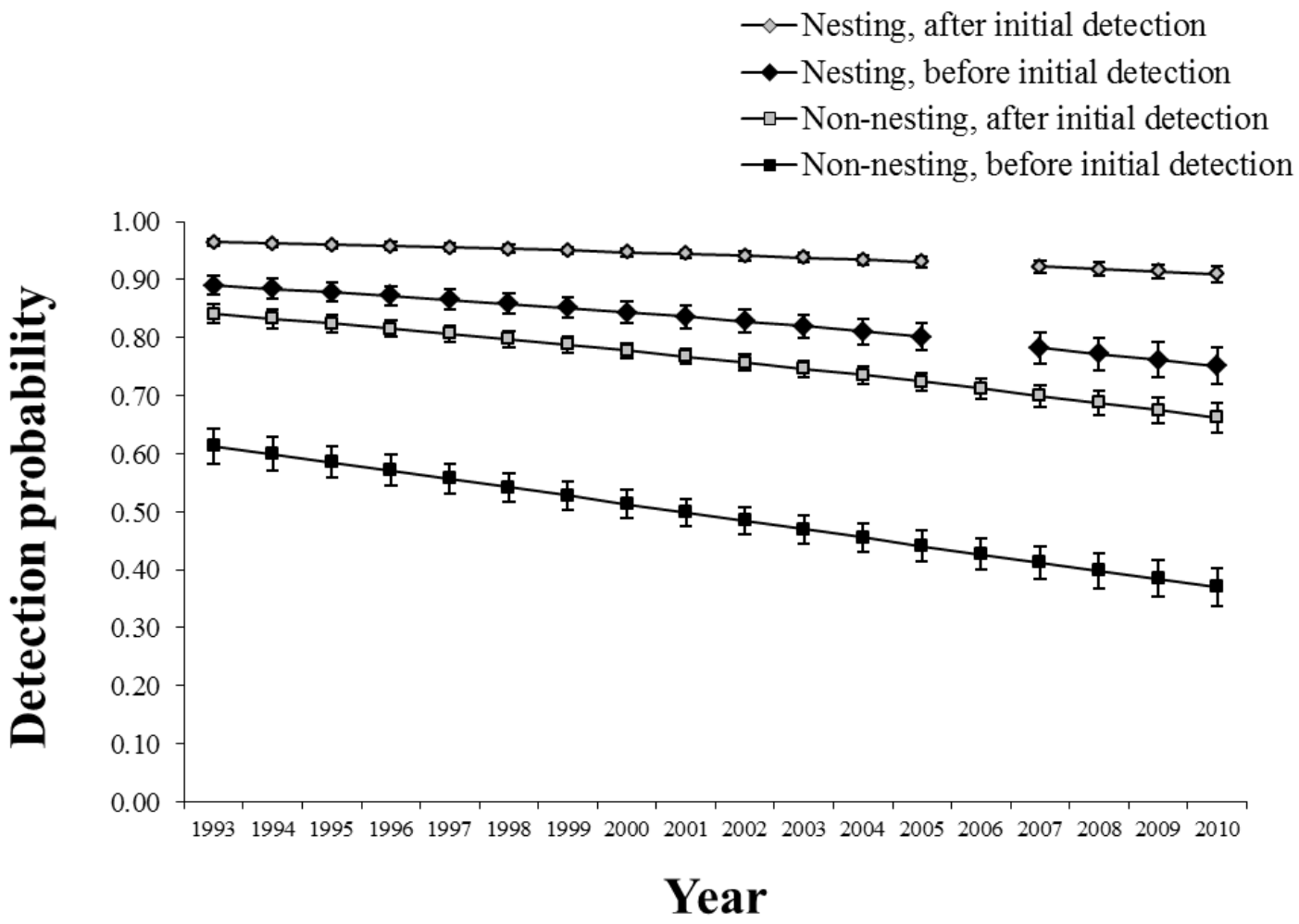

Nesting, after initial detection
Nesting, before initial detection
Non-nesting, after initial detection
Non-nesting, before initial detection
Detection probability
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010
Year

Figure 1.2. Annual estimates (SE) of territory extinction, colonization, and occupancy at California spotted owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1993-2010.

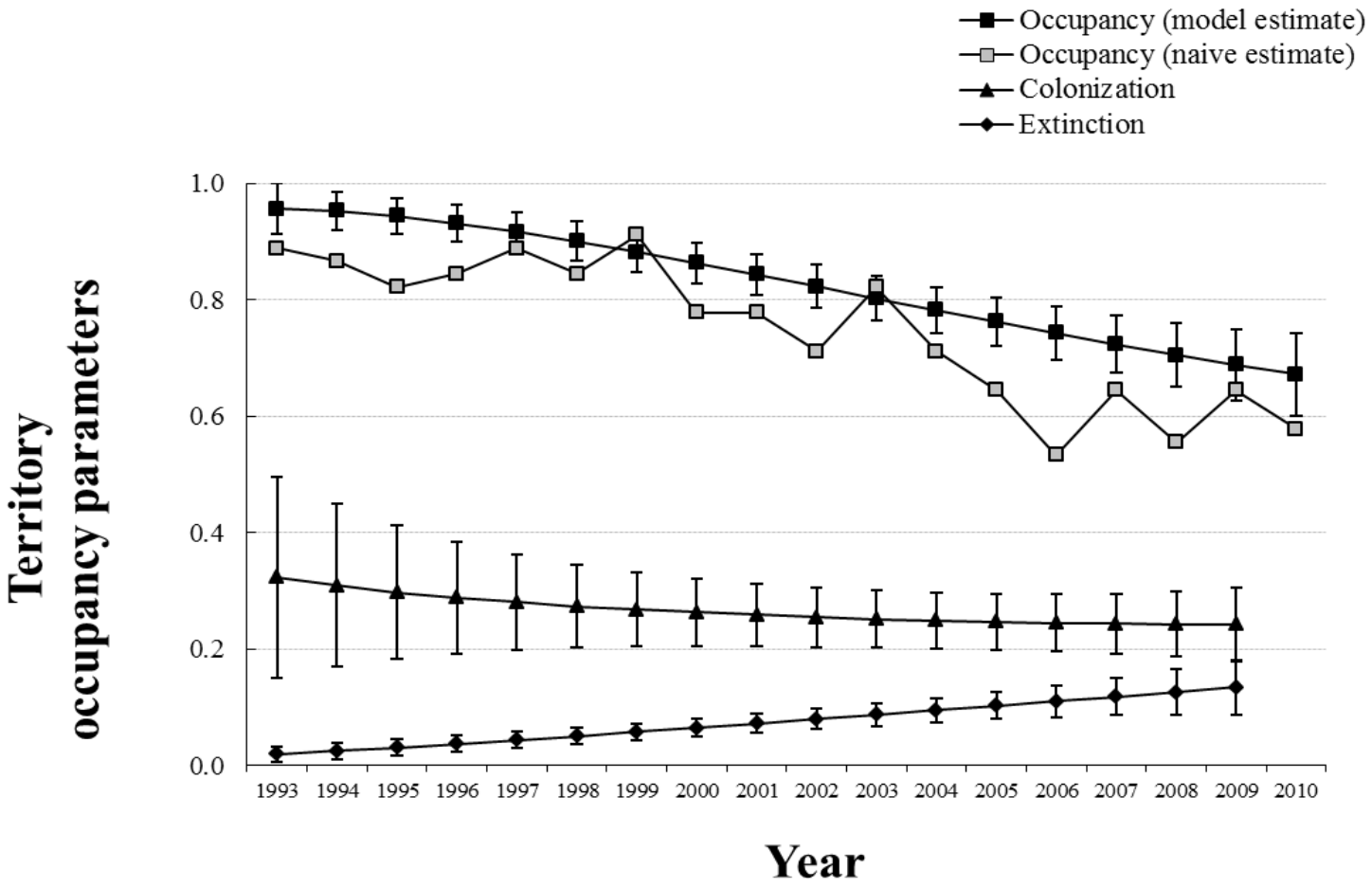

Occupancy (model estimate)
Occupancy (naive estimate)
Colonization
Extinction
Territory occupancy parameters
1.0
0.8
0.6
0.4
0.2
0.0
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
Year

Figure 1.3. Annual estimates (SE) of survival, recruitment, and finite rate of population change for a California spotted owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993-2009.

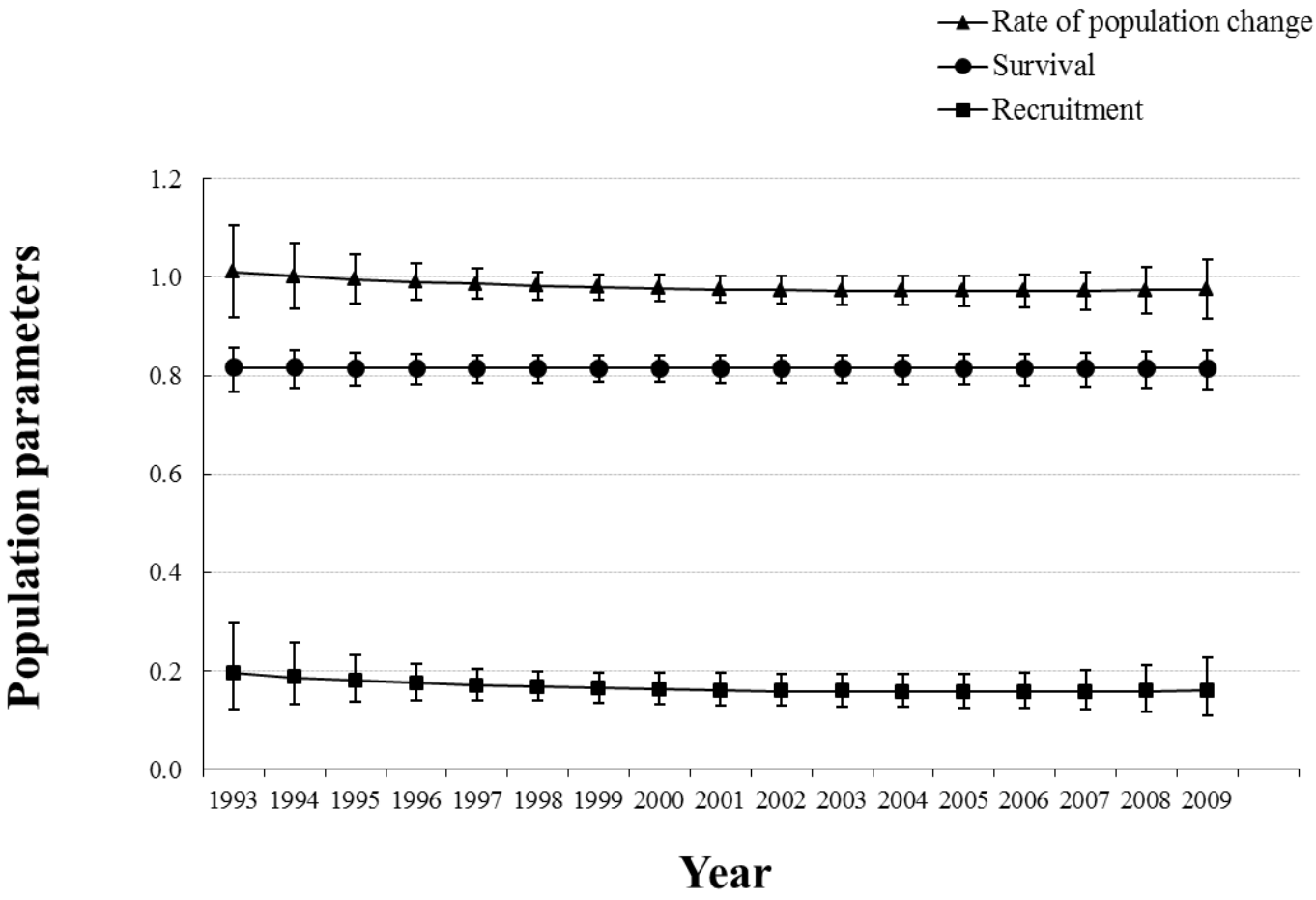
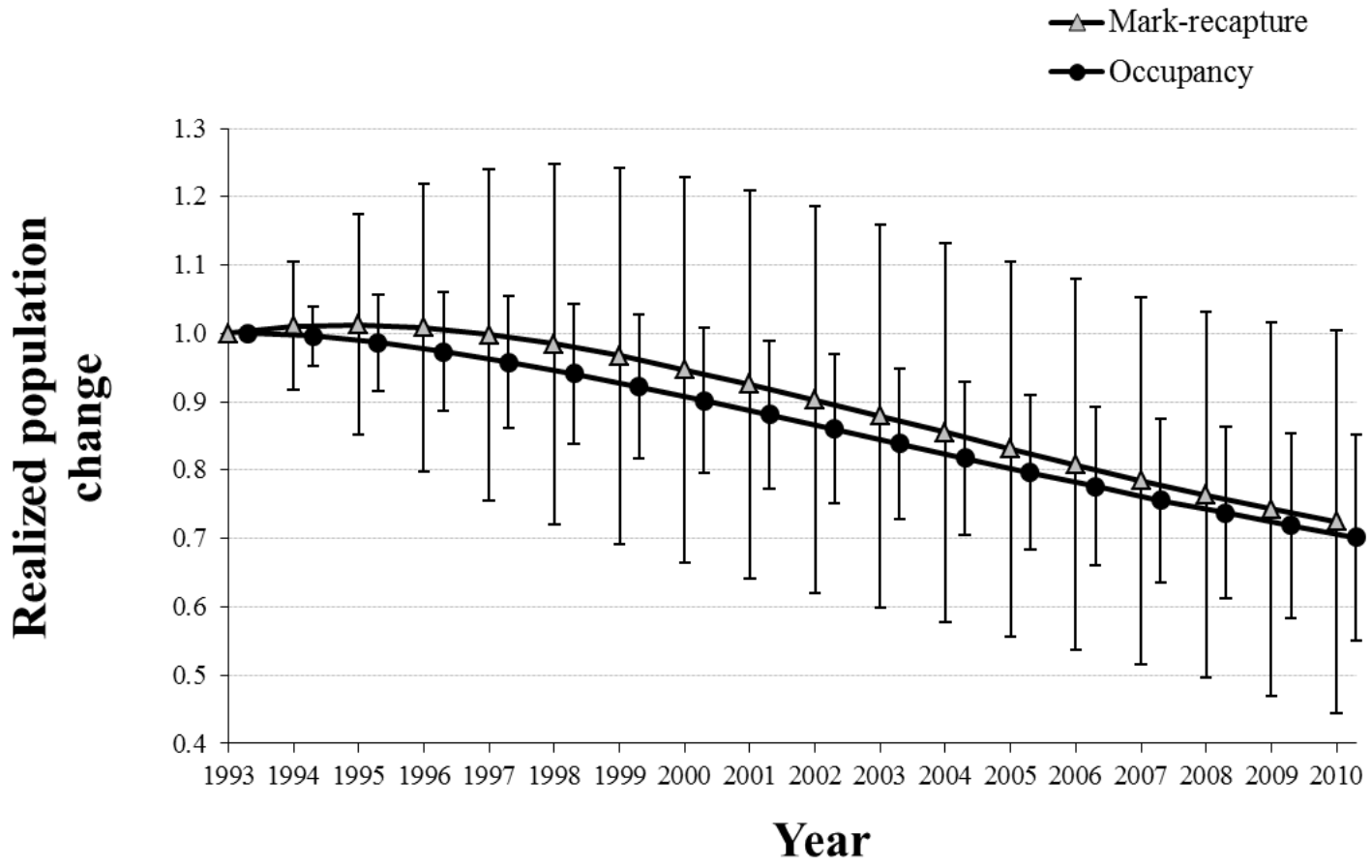

Rate of population change
Survival
Recruitment
Population parameters
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009
Year

Figure 1.4. Realized population change (95% CI) with both occupancy and mark-recapture data for a California spotted owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993-2010.


Mark-recapture
Occupancy
Realized population change
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010
Year

CHAPTER 2

AN INTEGRATED POPULATION MODEL FOR A DECLINING POPULATION OF CALIFORNIA SPOTTED OWLS

The California spotted owl (*Strix occidentalis occidentalis*) is a focal management species in the Sierra Nevada because of its use of late-seral forests. The status of this population has been uncertain for two decades because estimates of finite rates of population change have been relatively imprecise. I used an integrated population model (IPM) to obtain estimates of population change for a spotted owl population in the central Sierra Nevada because IPMs may improve the precision of parameter estimates. My IPM incorporated count, reproductive, and mark-recapture data over a 23-year period in a unified analysis. I observed a significant population decline in my study population, as evidenced by the geometric mean of the finite rate of population change ($\widehat{\overline{\lambda t}}$ = 0.969, 95% CRI 0.957, 0.980) and the resulting realized population change (proportion of the initial population present in 2012; $\hat{\Delta}_{2012}$ = 0.501, 95% CRI 0.383, 0.641). I could not distinguish whether my study area contained sink habitat or that the decline was indicative of one occurring throughout the Sierra Nevada because I lacked information on juvenile emigration from my study area. Thus far, the IPM literature has focused primarily on model development and evaluation, but my results suggested that the IPM framework has great potential for conservation applications, particularly for long-lived species whose annual rates of population change are near 1.0. My results also suggested

that continued monitoring of this population and reconsideration of the California spotted owl's status under the U. S. Endangered Species Act may be warranted.

INTRODUCTION

It can be difficult to detect population declines in species that are at conservation risk because, being rare, they are difficult to sample (Thompson 2004). Thus, analytical approaches that reduce uncertainty in parameter estimation can strengthen inferences regarding population trends in such species. Integrated population modeling (IPM) is one approach that can be used when independent data sources (e.g., count data, mark-recapture) are available (Besbeas et al. 2002, Schaub and Abadi 2011). Rather than analyzing each dataset separately, an IPM links population size to demographic rates using a demographic model (e.g., a Leslie matrix) and the likelihoods of the individual data sets. Statistical inference is then based on the joint likelihood (i.e., multiplication of the individual likelihoods). Some of the individual likelihoods will typically share one or more parameters, and the IPM's efficient use of all information on these parameters can lead to improved precision of the parameter estimates. An IPM also allows one to account for all sources of uncertainty in the parameter estimates and to estimate demographic parameters for which no explicit data are available (Schaub and Abadi 2011).

The status of the California spotted owl (*Strix occidentalis occidentalis*) in the Sierra Nevada has been uncertain for more than two decades despite the results of large mark-recapture studies, partly because of a lack of precision for population change

estimates (Franklin et al. 2004, Blakesley et al. 2010). Such uncertainty contributed to prior decisions not to list the California spotted owl as a threatened species under the Endangered Species Act (U.S. Fish and Wildlife Service 2003, 2006). The legal status of the California spotted owl has important consequences for the U.S. Forest Service (USFS) because it is the public land management agency that manages most of the species' habitat. The USFS has designated the California spotted owl a "sensitive" species, has funded several long-term demographic studies, and has implemented two major management plans over the past 20 years to protect the species and its habitats (Verner et al. 1992, U.S. Forest Service 2004). If California spotted owl populations have declined despite these plans, management strategies may need to be modified or new ones implemented.

Thus, I developed an IPM to estimate population change over a 23-year period in a demographically open California spotted owl population in the central Sierra Nevada (Seamans et al. 2001, Franklin et al. 2004, Blakesley et al. 2010). Repeated surveys at California spotted owl territories were conducted each year, individual owls were marked and resighted, and reproductive output was assessed for all territorial spotted owls. My IPM incorporated three types of data provided by these surveys—reproductive output, survival, and population counts. My approach was in contrast to all earlier studies of spotted owls that have relied solely upon either mark-recapture or occupancy data to estimate population change (e.g., Gutiérrez 1994, Forsman et al. 2011). By using an IPM framework, I hoped to achieve improved precision for population change estimates and thus reduce uncertainty about the status of my study population.

STUDY AREA

I conducted my study on a contiguous 35,500-ha area on the Eldorado National Forest in the central Sierra Nevada, California. The EDSA has been the site of a long-term mark-recapture study of California spotted owls (Seamans et al. 2001; Franklin et al. 2004; Blakesley et al. 2010). The entire area was surveyed each year regardless of land cover, topography, access, or land ownership. Approximately 60% of the EDSA was public land managed by the USFS, and 40% was private land managed by timber companies.

The primary vegetation type on the EDSA was mixed-conifer forest dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). Common understory species included California black oak (*Quercus kelloggii*), bigleaf maple (*Acer macrophyllum*), and tanoak (*Lithocarpus densiflorus*). Red-fir (*A. magnifica*) forest, dominated by red fir and lodgepole pine (*P. contorta*), occurred at higher elevations. Other local vegetation types and landscape features included chaparral, black oak woodland, and barren rock. Elevations on the EDSA ranged from 360 to 2400 m, and the climate was characterized by cool, wet winters and warm, dry summers.

METHODS

Spotted Owl Surveys

Surveys were conducted annually for spotted owls from 1986-2012 during their breeding season (1 April–31 August). Although the entire EDSA was not fully surveyed until 1993 (see Chapter 1), I used all data from 1990-2012 because my analytical approach was sufficiently flexible to accommodate data from years having different survey effort. For example, I used a Bayesian analysis for the multi-state occupancy model (see below) in which the true state of a sampling unit (i.e., territory) was imputed for each iteration of the Markov chain as a useful byproduct of estimating the transition probabilities and other parameters (MacKenzie et al. 2009). Thus, estimates of reproductive output and the number of adults were extrapolated for territories that were not surveyed in a given year.

Spotted owl surveys consisted of imitating vocalizations (vocal lures) for 10 minutes at designated survey stations or while walking along survey routes. The sex of each responding spotted owl was determined by the pitch of its 4-note territorial call; males have a lower-pitched call than females (Forsman et al. 1984). If spotted owls were detected on nocturnal surveys, diurnal surveys were conducted to locate and band unmarked individuals, resight marked individuals, and assess reproduction (Franklin et al. 1996). Spotted owls were banded with a numbered locking metal band on one leg and a unique combination of color band and color tab on the other leg (Franklin et al. 1996).

Analytical Design

I used an age-structured population IPM similar to the model developed by Abadi et al. (2010a) for the little owl (*Athene noctua*). The data used in the IPM consisted of

annual population counts of adults (*y*), annual reproductive output (*J*), and mark-recapture data for young and adults (*m*) (Fig. 1; Appendix 1). The population parameters contained in the IPM were apparent adult and juvenile survival (φ_{juv} and φ_{ad}), reproductive rate (*f*), immigration rate (*imm*), and population size (*N*). I was able to estimate immigration rates of new adults onto the study area despite the lack of explicit data on immigration (Abadi et al. 2010a). Rather than simply using the naïve counts of the number of adults (*y*) and young (*J*) within the population, I first used a multi-state occupancy model that incorporated imperfect detection to obtain less biased annual estimates of the number of adults and young (MacKenzie et al. 2009). Note that *R* (the number of adults for which reproduction was assessed) in Fig. 1 was equivalent to *y* because the multi-state occupancy model estimated both the number of adults and young at each territory.

Multi-state Occupancy Model

I used a dynamic, multi-state occupancy model to estimate the number of fledgling and adult spotted owls on the EDSA each year. The sampling units were the owl territories; I considered a territory to be a site where spotted owls were observed either roosting or nesting. Each territory could be in one of five true states: 0 = no spotted owls present; 1 = single adult present; 2 = adult pair present, no young produced; 3 = adult pair present, one young produced; 4 = adult pair present, two young produced. Three young were rarely produced (four times in 23 years), so I did not include a sixth state with three young. I considered definitive evidence of reproduction to be an

observation of young, either at the nest or elsewhere in the nest stand. I included both nocturnal and diurnal surveys in the analyses. Surveys in which no spotted owls were detected had to be ≥ 30 minutes in total duration to be considered adequate for inclusion in the database. I did not include nocturnal detections that were > 400 m from long-term core use areas (Berigan et al. 2012) because these individuals may have been individuals from a neighboring territory or non-territorial "floaters".

When constructing the database, I divided each breeding season into 10 semimonthly periods (1-15 April, 16-30 April, 1-15 May, 16-31 May, etc.). During each survey period, I recorded the highest occupancy state (0, 1, 2, 3, or 4) observed at each territory; the observed occupancy state may have been less than or equal to the true value. On surveys conducted before 1 June, I constrained the probabilities of detecting reproduction (states 3 and 4) to 0 because reproduction was observed before this date on only 5 occasions during the 23-year study period. If a territory was not surveyed during a semimonthly survey period, I treated it as a missing observation. The primary sampling periods were breeding seasons (i.e., years), and the secondary sampling periods were the semimonthly periods within each breeding season.

I used the model parameterization that contained parameters for initial occupancy, transition probability, and detection probability (MacKenzie et al. 2009). The initial occupancy vector contained the probabilities that a territory was in a specific true state in the first year of the study. The transition probability matrix (TPM) contained the probabilities of a territory being in a specific true state at time $t + 1$ given its true state at time t. Similarly, the detection probability matrix contained the probabilities that a

territory was observed in a specific state given its true state during that year. As noted above, I assumed that a territory could not be observed in a state higher than its true state. Thus, the model parameters were as follows:

$\varphi^{[m]}$ = the probability that a territory was in state *m* in the initial year;

$\varphi_t^{[m,n]}$ = the probability that a territory in state *m* in year *t* was in state *n* in year *t* + 1;

$p_{j,t}^{l,m}$ = the probability of observing a territory in state *l* during survey period *j* of year *t* given that its true state was *m*.

Related sets of parameters (initial occupancy probabilities, detection and transition probabilities for a specific state) were constrained to sum to 1. For example, the individual probabilities that a territory in true state *m* in year *t* was in one of the five states in year *t* + 1 ($\varphi_t^{[m,0]}$, $\varphi_t^{[m,1]}$, $\varphi_t^{[m,2]}$, $\varphi_t^{[m,3]}$, $\varphi_t^{[m,4]}$) must sum to 1. Similarly, the individual detection probabilities for a territory in true state *l* during a given year and survey period must sum to 1, keeping in mind that a territory cannot be observed in a state higher than its true state. Thus, if a territory was in true state 3 during year *t*, then $p_{j,t}^{0,3}$, $p_{j,t}^{1,3}$, $p_{j,t}^{2,3}$, and $p_{j,t}^{3,3}$ must sum to 1 for each survey period *j*.

I implemented a state-space modeling approach similar to MacKenzie et al. (2009). State-space models contain two components—a submodel for the latent, state process (e.g., the occupancy model described above) and a submodel for the observation process in which the observed data are conditional on the unobserved or partially observed state process (Buckland et al. 2004). I considered the true state of each territory each year to be a latent (unknown) variable and predicted or imputed its true

state from the observed data using Markov chain Monte Carlo (MCMC) methods within a Bayesian framework (Link et al. 2002). As noted by MacKenzie et al. (2009), an advantage of the state-space approach is that relevant summaries of the system (e.g., the number of territories in each state) can be calculated easily. I estimated the number of fledglings produced each year (J) and the number of adults in the population each year (y) as:

J = no. of territories in state 3 + [2 × (no. of territories in state 4)]

y = no. of territories in state 1 + [2 × (no. of territories in states 2, 3, or 4)]

For related model parameters that were constrained to sum to 1 (see above), a Dirichlet prior distribution is appropriate. The Dirichlet is a multivariate generalization of the beta distribution and the conjugate prior for multinomial distributions (McCarthy 2007). However, the parameters of a Dirichlet distribution cannot be stochastic nodes in OpenBUGS software, so I induced a Dirichlet distribution (Spiegelhalter et al. 2003). For each model parameter (i), I specified an associated variable (β_i) with a gamma distribution. Then for a group of related model parameters, I set each parameter equal to $\beta_i/\sum_{k=1}^{N}\beta_k$ where N was the total number of parameters within the group; this ensured that their sum was 1 (Spiegelhalter et al. 2003). I incorporated annual random effects for all detection and transition probabilities by specifying uninformative distributions (i.e., hyperparameters) for the parameters of the gamma distribution within a related group of β_i's (Spiegelhalter et al. 2003). The gamma distributions were characterized by a shape parameter (r) and a rate parameter (ν) (McCarthy 2007); I specified a uniform distribution for all r's and a gamma distribution for all ν's.

I held within-year detection probabilities constant to keep the number of estimated parameters at a manageable level, except I constrained the probability of detecting reproduction before 1 June to 0 (see above; MacKenzie et al. 2009). I specified an uninformative, uniform prior distribution for detection probabilities when a territory's true state was 1 and thus had only two possible outcomes (single owl was detected or not detected).

I conducted the analysis using OpenBUGS (Lunn et al. 2009; see Appendix 2 for model code). I ran three chains of 50,000 iterations to approximate the posterior distributions of the model parameters after discarding the initial 10,000 iterations of each chain as a burn-in period. After the burn-in period, the chains were well-mixed as the Gelman-Rubin convergence statistic ($\hat{R}$) was < 1.1 for all parameters (Gelman and Hill 2007).

Integrated Population Model

The modeled population consisted of three age classes (juvenile, 1 year old, ≥ 2 years old). I hereafter refer to any owls at least one year old as "adult" spotted owls. Non-juvenile spotted owls can be distinguished into 3 age classes (1 year old, 2 years old, and ≥ 3 years old) based on the appearance of their rectrices (Moen et al. 1991). However, prior analyses using Cormack-Jolly-Seber models (Seber 1982) showed that differences in annual survival among these three age classes were small (< 0.10; unpublished data); 1- and 2-year-olds also comprised < 10% of the total population on average (unpublished data). Furthermore, I did not use a female-only model because

single spotted owls at territories were typically male and a potentially important component of the total population size. I modeled the total population of males and females combined, instead of separate population components for each sex, because another occupancy state would have been required to distinguish between single males and single females, but data were sparse for single females.

As noted above, I used the estimates of *y* and *J* provided by the multi-state occupancy model, rather than naïve counts of young and adults, to account for imperfect detection. The mark-recapture data were summarized as *m*-arrays (Burnham et al. 1997) for juveniles and adults. This format allowed much faster computation but reduced the flexibility of the modeling (i.e., individual covariates could not be used). The data sets were not independent, which is an assumption of the IPM, but Abadi et al. (2010b) demonstrated with simulations that using non-independent data for a similar IPM resulted in minimal bias in the parameter estimates. In addition, they observed increased precision and accuracy in parameter estimation when all three sources of data were analyzed simultaneously, rather than individually.

I again used a state-space approach where the state process was described by the following distributions:

$$N_{1,t+1} \sim \text{Poisson}([N_{1,t} + N_{2,t}] \times f_t \times \varphi_{juv,t})$$

$$N_{2,t+1} \sim \text{Binomial}([N_{1,t} + N_{2,t}], \varphi_{ad,t}) + \text{Poisson}([N_{1,t} + N_{2,t}] \times imm_t)$$

where $N_{1,t}$ was the number of 1-year-old spotted owls at time t; $N_{2,t}$ was the number of spotted owls ≥ 2 years old at time t; φ_{juv} and φ_{ad} were the apparent survival probabilities of juveniles and adults, respectively, from time t to $t + 1$; f_t was the

reproductive output per adult at time t; and imm_t was the immigration rate (number of immigrant adult spotted owls into the population at time t +1 per adult in the population at time t). Thus, the expected number of 1-year-old spotted owls at time t + 1 was the product of the number of young produced at time t and apparent juvenile survival from t to t + 1. The expected number of spotted owls ≥ 2 years old at time t +1 had two components: 1) the number of adults at time t multiplied by apparent adult survival from t to t +1, and 2) the number of adults at time t multiplied by the immigration rate from t to t + 1. As noted by Abadi et al. (2010a), immigrants were assumed to enter the population as individuals ≥ 2 years old, but the results would be identical if they were assumed to enter as 1-year-olds. The total population size (N_t) was the sum of $N_{1,t}$ and $N_{2,t}$. I estimated the finite rate of population change (λ_t) as N_{t+1}/N_t and the realized population change (Δ_t) as N_t/N_1.

I specified a Poisson distribution for the "count" data (J, y), which allowed the absolute observation error to change proportionally with the number of estimated adults and juveniles. For the mark-recapture data formatted as m-arrays, I used the Cormack-Jolly-Seber (CJS) model with a product multinomial distribution for the estimation of φ_{juv} and φ_{ad} (Kéry and Schaub 2012). Recapture probabilities (p; not to be confused with detection probability in the occupancy model) were also estimated within the CJS model. I incorporated annual random effects by assuming that all demographic parameters and p were realized from normally distributed variables that were transformed to real values by the logit link function for survival and recapture rates and by the log link function for reproductive output and immigration rates (Abadi et al. 2010a, Kéry and Schaub 2012).

For each variable that would be transformed into the appropriate demographic parameter or *p*, I estimated the mean and variance as hyperparameters from normal distributions (Kéry and Schaub 2012).

I again used MCMC methods in a Bayesian framework to impute the true states from the data. I conducted the IPM analyses using R2WinBUGS (Sturtz et al. 2005), a package available in program R 2.15 (R Core Team 2013) that calls WinBUGS (Lunn et al. 2000) for processing the data and model script in batch mode (see Appendix 3 for model code). I ran three chains of 20,000 iterations to approximate the posterior distributions of the model parameters and discarded the initial 10,000 iterations of each chain as a burn-in period. The chains were well-mixed after the burn-in period ($\hat{R} < 1.1$ for all parameters).

RESULTS

Multi-state Occupancy

I identified 45 spotted owl territories on the EDSA from 1990-2012, so the maximum potential population size of territorial spotted owls was 90 individuals (i.e., if all territories were occupied by a pair of owls). Survey coverage increased during the early years of the study, as evidenced by the number of territories that were surveyed at least once each year ($\leq$ 37 territories from 1990-1992, $\geq$ 41 from 1993-1995, $\geq$ 44 from 1997-2012). In the initial year (1990), nearly all surveyed territories were occupied by pairs ($\hat{\varphi}^{[0]}$ = 0.02, 95% CRI 0.00-0.15; $\hat{\varphi}^{[1]}$ = 0.02, 95% CRI 0.00-0.17; Table 1). The estimated number of territorial adults in the population declined steadily from a

maximum of 88 (95% CRI 76-90) in 1990 to a minimum of 42 (95% CRI 39-49) in 2012 (Fig. 2). The estimated number of young produced varied more substantially but also declined over the study (Fig. 2), which was expected given the declining number of adults available to breed.

The probability of detecting at least one spotted owl on a survey (i.e., 1 – probability of not detecting any spotted owls) was ≥ 0.72 for all occupancy states except territories with single spotted owls where non-detection rates were high ($\hat{p}^{0,1}$ = 0.72, 95% CRI 0.64-0.80). Additionally, the probability of detecting at least one spotted owl increased with the state of a territory (Table 1).

The probability of a territory being unoccupied depended upon the territory's state in the previous year, ranging from 0.31 (95 % CRI 0.24, 0.38) for a territory that was unoccupied in the previous year to 0.14 (95% CRI 0.11, 0.18) for a territory occupied by a pair that produced two young in the previous year (Table 1). Conversely, a territory was more likely to be occupied by a pair (states 2, 3, and 4) if the territory was also occupied by a pair in the previous year (Table 1). However, there was no evidence for a cost of reproduction in that spotted owls were as likely to reproduce (states 3 and 4) in territories that were in states 3 or 4 the previous year as they were in territories that were occupied by a non-breeding pair (state 2) the previous year (Table 1).

Integrated Population Model

The annual estimates of population size were close to the "counts" provided by the occupancy model (Fig. 2). Thus, the observation error was small, which was

expected given that the "counts" had already been rigorously modeled to account for imperfect detection. The finite rate of population change ($\hat{\lambda}_t$) was < 1.0 in every year except for two years (1992, 1993) early in the study period (Fig. 3), and the geometric mean of $\hat{\lambda}_t$ was clearly < 1.0 ($\widehat{\overline{\lambda t}}$ = 0.969, 95% CRI 0.957, 0.980). As a result, the population declined by 50% from 1990-2012 ($\hat{\Delta}_{2012}$ = 0.501, 95% CRI 0.384, 0.642; Fig. 4).

Annual estimates of adult survival ($\hat{\varphi}_{ad,t}$) ranged from 0.805-0.843 (Fig. 5); mean adult survival over the entire study period was 0.828 (95 % CRI 0.801, 0.854). In contrast, annual estimates of juvenile survival ($\hat{\varphi}_{juv,t}$) ranged from 0.075-0.129 (Fig. 5) with a mean value of 0.087 (95% CRI 0.049, 0.129). Immigration rates ($\widehat{imm}_t$) were similar to juvenile survival rates, ranging from 0.097-0.105 with a mean value of 0.097 (95% CRI 0.055, 0.140; Fig. 6). Reproductive output per adult ranged from 0.324-0.546 (Fig. 6), and the mean reproductive output per adult was 0.411 (95% CRI 0.361, 0.462). Annual recapture probabilities from the CJS model were high ($\overline{\hat{p}}$ = 0.868, 95% CI 0.821, 0.911) and exhibited low temporal variation.

DISCUSSION

My study population of California spotted owls clearly declined from 1990-2012 as the estimated realized population change was 50% with 95% credible intervals that were well below 1.0. My use of an integrated population model resulted in more precise estimates of realized population change ($\hat{\Delta}_{2012}$ = 0.501, 95% CRI 0.384–0.642) when compared to the realized population change estimate from my analysis of the mark-

recapture data (Chapter 1; Δ_t = 0.725, 95% CI 0.445–1.004). However, I did not account for covariance among the demographic rates in my IPM, which may have resulted in "false" precision (i.e., underestimation of the true variance). If covariances are incorporated into the IPM (e.g., Schaub et al. 2013), IPMs have excellent potential as a tool for assessing the status of species of conservation or management concern. The annual rates of California spotted owl population change that I observed were consistently just below 1.0 (Fig. 3), but over a 23-year period the cumulative effect of these annual declines resulted in a loss of half the initial population. I would expect that declining populations of species with similar life history strategies (long-lived, having high annual survival and low reproductive rates) would also exhibit gradual declines and that IPMs could be useful for detecting declining trends in such species. Although I analyzed a long-term (and thus relatively large) dataset, the flexibility and potential gains in precision afforded by IPMs should also be important in situations where data are sparse (Schaub et al. 2007).

Apparent survival of adult California spotted owls was high ($\overline{\hat{\varphi}}_{ad}$ = 0.828, 95 % CRI 0.801–0.854) and showed little temporal variation, which was consistent with prior results for both California and northern (*S. o. caurina*) spotted owls (LaHaye et al. 2004, Blakesley et al. 2010, Forsman et al. 2011). In contrast, apparent survival of juveniles was only 0.086 (95% CRI 0.048–0.129), which was markedly lower than that reported by LaHaye et al. (2004) (0.368, SE 0.038). However, apparent survival was a function of both mortality and emigration from the study area, and LaHaye et al. (2004) studied an insular population of California spotted owls where juvenile emigration was negligible.

Using data from this same insular population, Zimmerman et al. (2007) demonstrated that artificially varying the size of the study area had a major effect on estimates of apparent juvenile survival but no effect on estimates of apparent adult survival. Their juvenile survival estimates ranged from 0.08 (SE 0.03) on their smallest "study area" to 0.33 (SE 0.03) on their largest "study area." Thus, I suspect that juvenile emigration from the EDSA was substantial, but its magnitude was unknown because I lacked information on radio-marked juveniles (see Burnham et al. 1996). I note, however, that juvenile emigration did not bias the IPM population size estimates because the IPM was constructed to represent an open population (i.e., immigration and emigration were component processes of the IPM).

Although survival of adult California spotted owls varied less than reproductive output, the two parameters made similar contributions to variation in population change. This finding was consistent with the results of Seamans and Gutiérrez (2007a), who used data collected from my study area within a female-based population projection matrix. They also found that adult survival exhibited low temporal variation relative to reproductive output but that the two parameters made similar contributions to λ, which was much more sensitive to changes in adult survival. My results supported the hypothesis that California spotted owls evolved a life-history strategy that favors longevity to increase the likelihood of experiencing favorable years for reproduction, which can be strongly influenced by annual climatic conditions (Seamans and Gutiérrez 2007a, Franklin et al. 2000).

I did not include habitat-related covariates in my IPM for any of the demographic parameters, so it was unclear what factors were related to the decline of my study population. One potential explanation was that habitat quality declined within the EDSA over the past 20 years because timber harvest and wildfire reduced the amount of forest containing large trees and dense canopies. For example, Seamans and Gutiérrez (2007b) found that loss of California spotted owl habitat was negatively correlated with territory colonization and positively correlated with dispersal of breeding individuals to other territories. Another possible explanation was that climatic conditions were not conducive to high reproductive rates during the study period. If reproductive rates were to increase in future years, the population might stabilize and even grow. However, I was unable to distinguish between these two possibilities, which highlighted the need for additional research that quantifies habitat change on the EDSA during my study period and relates such change to variation in demographic parameters.

In conjunction with recent estimates of population decline on 2 other study sites within the Sierra Nevada ecosystem (Conner et al. 2013), my finding of a large, long-term decline in a California spotted owl population has potentially important ramifications for forest management in the Sierra Nevada. A primary goal of USFS management is the maintenance of viable California spotted owl populations (U.S.D.A. Forest Service 2004), and thus, it becomes imperative to understand why populations are declining and to develop management actions that reverse the decline. Moreover, it suggests that rigorous monitoring of this species should continue. In addition to the mark-recapture studies, the initiation of large-scale, occupancy-based monitoring

programs may offer a cost-effective means of assessing population trends and factors related to those trends throughout the Sierra Nevada (see Chapter 1). Finally, my results suggested that the U.S. Fish and Wildlife Service (2006) may need to reevaluate their recent decision not to list the California spotted owl under the Endangered Species Act because population declines are becoming apparent and it is not clear if USFS management actions are related to this decline.

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Table 2.1. Posterior means (95% CRI) of parameters from a multi-state occupancy model of California spotted owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1990-2012. The territory states are: 0 = no spotted owls present; 1 = single adult present; 2 = pair of adults present, no young produced; 3 = pair of adults present, one young produced; 4 = pair of adults present, two young produced.

Parameter	**Territory state**				
	0	1	2	3	4
Initial occupancy[a]:					
$\varphi^{[m]}$	0.02 (0.00, 0.15)	0.02 (0.00, 0.17)	0.52 (0.22, 0.75)	0.03 (0.00, 0.30)	0.41 (0.19, 0.66)
$p^{l,1}$	0.72 (0.64, 0.80)	0.28 (0.20, 0.36)	–	–	–
$p^{l,2}$	0.25 (0.21, 0.29)	0.25 (0.22, 0.29)	0.50 (0.45, 0.55)	–	–
$p^{l,3}$ (early)[c]	0.28 (0.23, 0.33)	0.29 (0.25, 0.34)	0.43 (0.37, 0.49)	–	–
$p^{l,3}$ (late)[d]	0.20 (0.16, 0.25)	0.22 (0.18, 0.27)	0.33 (0.27, 0.39)	0.25 (0.20, 0.30)	–
$p^{l,4}$ (early)[c]	0.25 (0.21, 0.30)	0.24 (0.20, 0.28)	0.51 (0.46, 0.56)	–	–

$p^{l,4}$ (late)[d]	0.13 (0.10, 0.16)	0.16 (0.13, 0.20)	0.23 (0.18, 0.28)	0.14 (0.11, 0.17)	0.34 (0.30, 0.38)
Transition probabilities[e]:					
$\varphi^{[0,n]}$	0.31 (0.24, 0.38)	0.24 (0.19, 0.29)	0.16 (0.13, 0.20)	0.15 (0.12, 0.19)	0.14 (0.11, 0.18)
$\varphi^{[1,n]}$	0.25 (0.21, 0.30)	0.23 (0.18, 0.28)	0.19 (0.15, 0.23)	0.17 (0.13, 0.21)	0.16 (0.13, 0.20)
$\varphi^{[2,n]}$	0.15 (0.12, 0.18)	0.16 (0.12, 0.19)	0.25 (0.20, 0.31)	0.19 (0.15, 0.23)	0.25 (0.21, 0.30)
$\varphi^{[3,n]}$	0.17 (0.13, 0.21)	0.17 (0.14, 0.21)	0.24 (0.19, 0.29)	0.20 (0.16, 0.25)	0.22 (0.17, 0.27)
$\varphi^{[4,n]}$	0.14 (0.11, 0.17)	0.14 (0.11, 0.18)	0.27 (0.22, 0.33)	0.21 (0.16, 0.26)	0.24 (0.16, 0.26)

---

[a] probability that a territory was in state *m* in the initial year.

[b] probability of observing a territory in state *l* given that its true state was 0, 1, 2, 3, or 4. For example, the entry for $p^{l,1}$ and territory state = 0 indicates the value for parameter $p^{0,1}$.

[c] early = surveys conducted prior to 1 June; the probability of detecting reproduction (i.e., observing young) was set to 0.

[d] late = surveys conducted on or after 1 June.

[e] probability that a territory in state 0, 1, 2, 3, or 4 in year *t* was in state *n* in year $t + 1$. For example, the entry for $\varphi^{[2,n]}$ and territory state = 0 indicates the value for parameter $\varphi^{[2,0]}$.

Figure 2.1. Graphic representation of an integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990-2012 (modeling framework adapted from Abadi et al. 2010a). R = number of adults assessed for reproduction; J = number of young produced, f = number of young produced per adult, *imm* = immigration rate (number of immigrants per adult), φ_{juv} = juvenile survival probability, φ_{ad} = adult survival probability, m = capture–recapture data, p = recapture probability, y = population count data, N = population size.

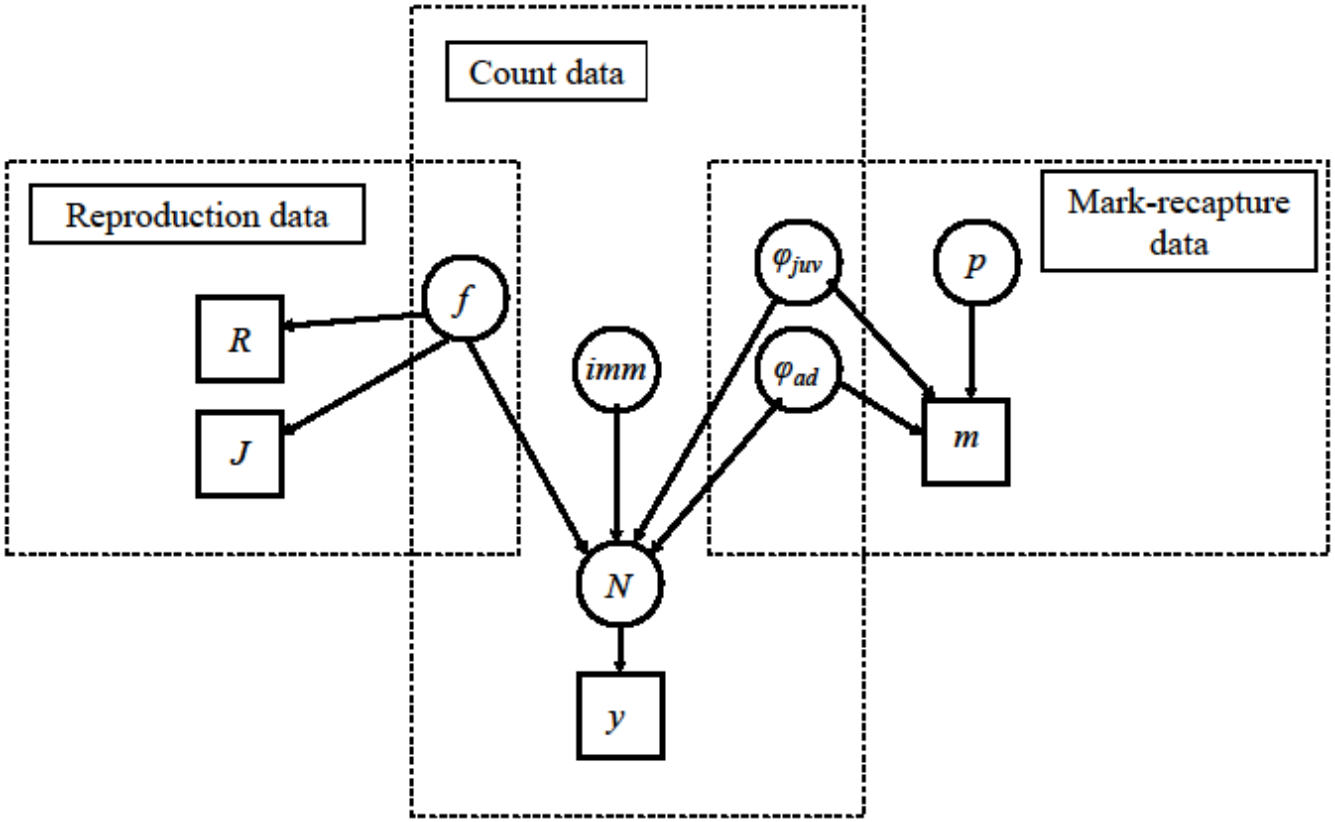

Count data
Reproduction data
Mark-recapture data
f
R
J
imm
φ_{juv}
φ_{ad}
p
m
N
y

Figure 2.2. Posterior means (95% CRI) of the annual number of territorial adults and young produced from a Bayesian multi-state occupancy model for a California spotted owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1990-2012. The posterior means of adult population size from an integrated population model incorporating these data are also shown.

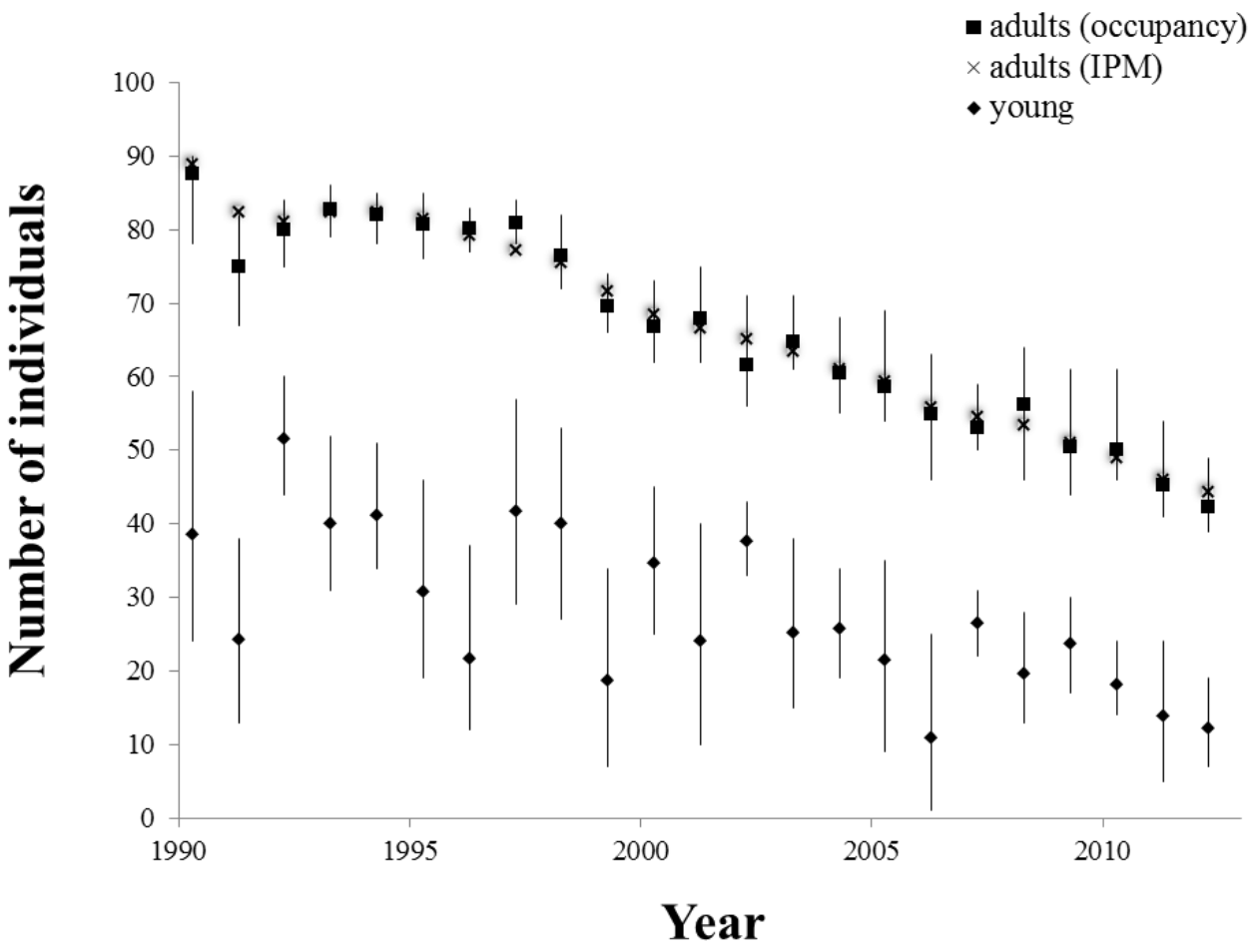

adults (occupancy)
adults (IPM)
young
Number of individuals
100
90
80
70
60
50
40
30
20
10
0
1990
1995
2000
2005
2010
Year

Figure 2.3. Posterior means of the finite rate of population change (λ) from a Bayesian integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990-2011.

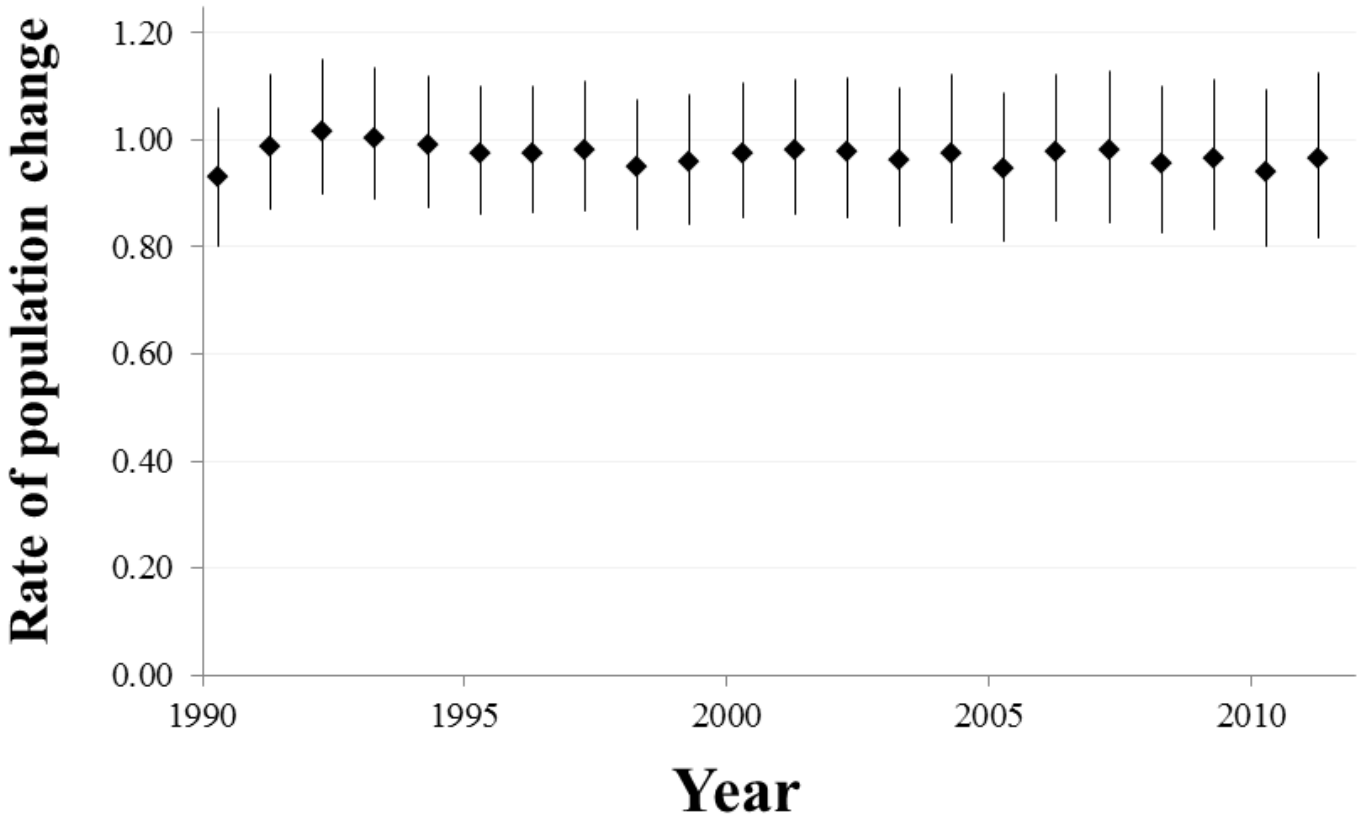

Rate of population change
1.20
1.00
0.80
0.60
0.40
0.20
0.00
1990
1995
2000
2005
2010
Year

Figure 2.4. Posterior means (95% CRI) of realized population change from a Bayesian integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990-2012.

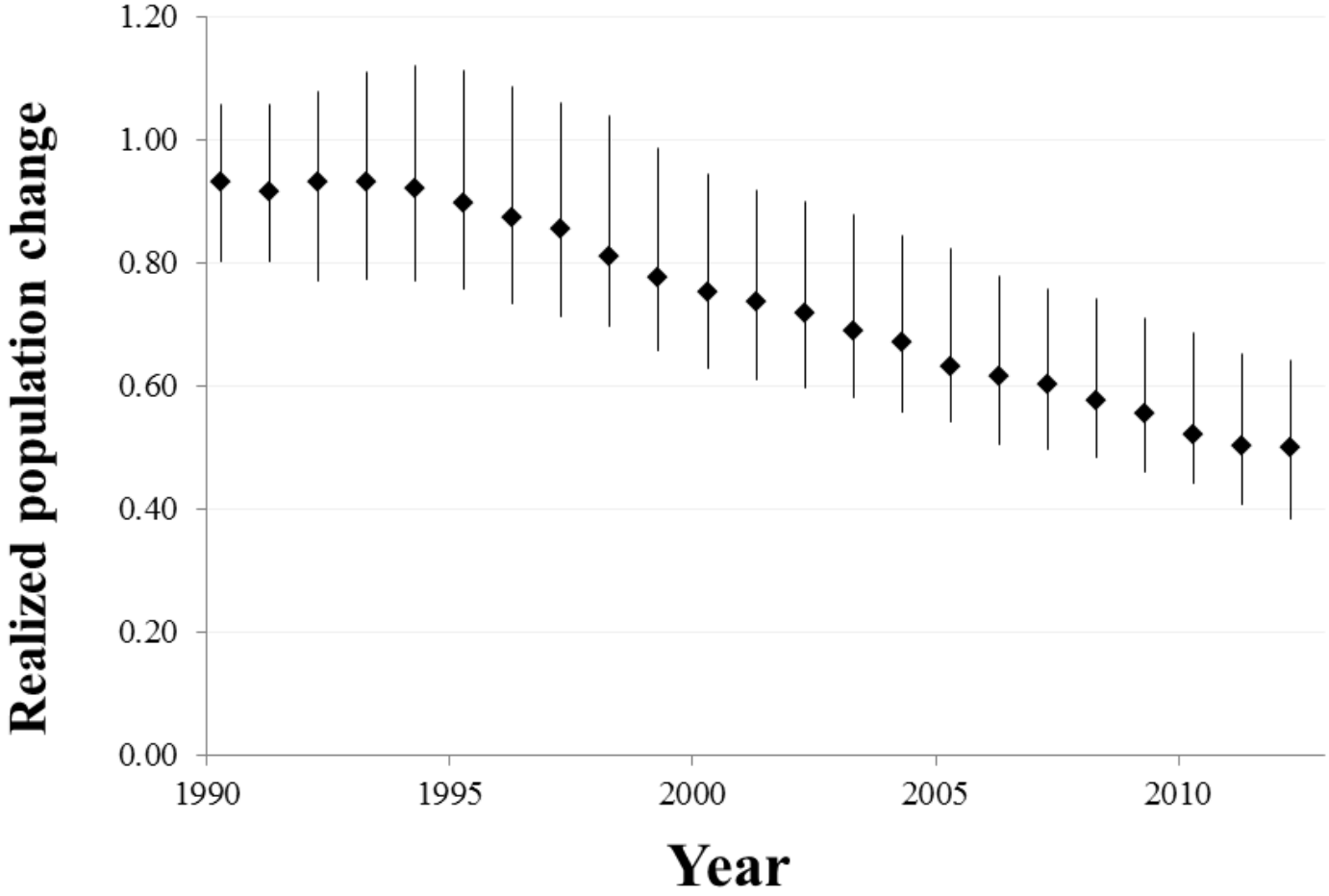

Realized population change
1.20
1.00
0.80
0.60
0.40
0.20
0.00
1990
1995
2000
2005
2010
Year

Figure 2.5. Posterior means of apparent adult survival and apparent juvenile survival from a Bayesian integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990-2011.

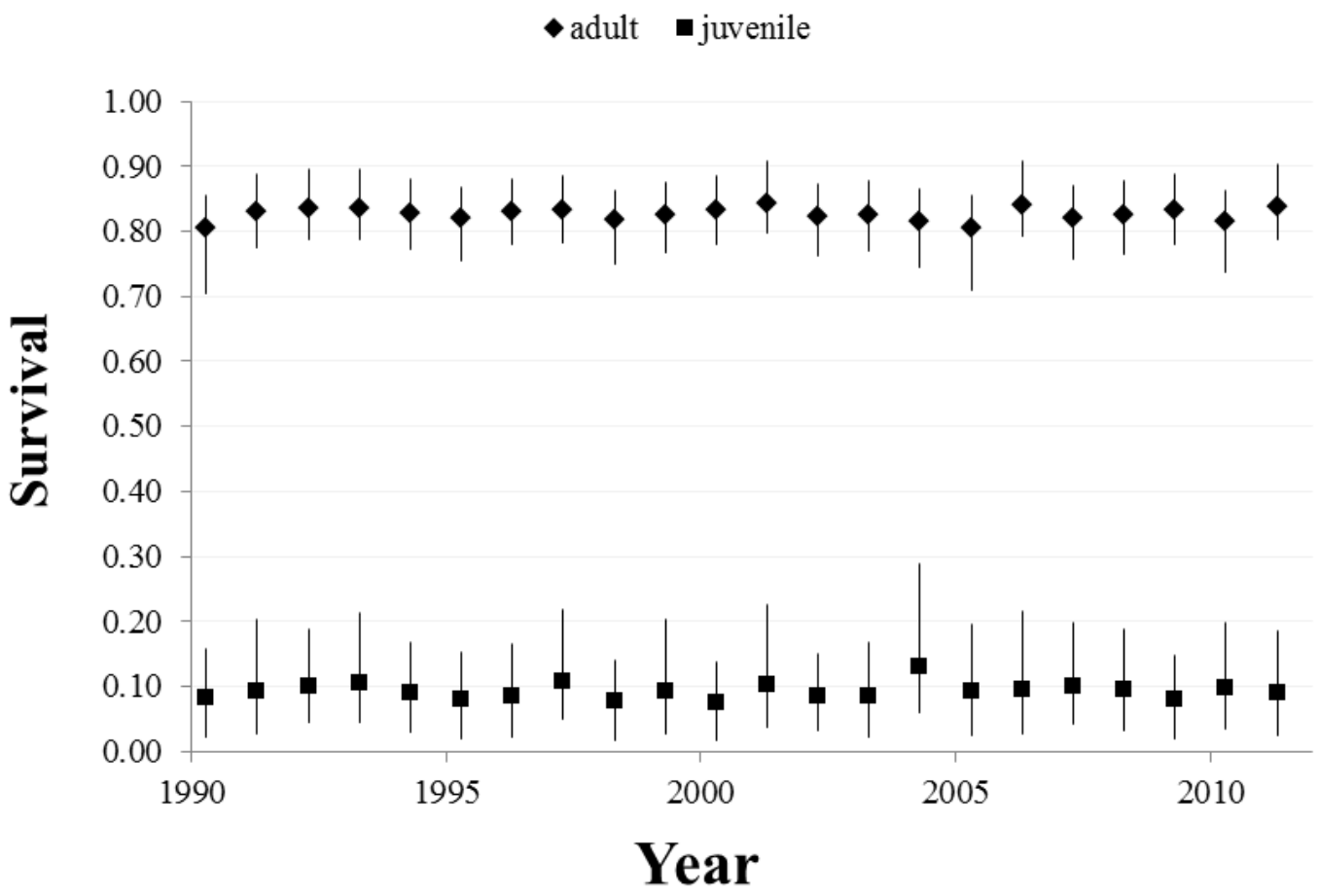
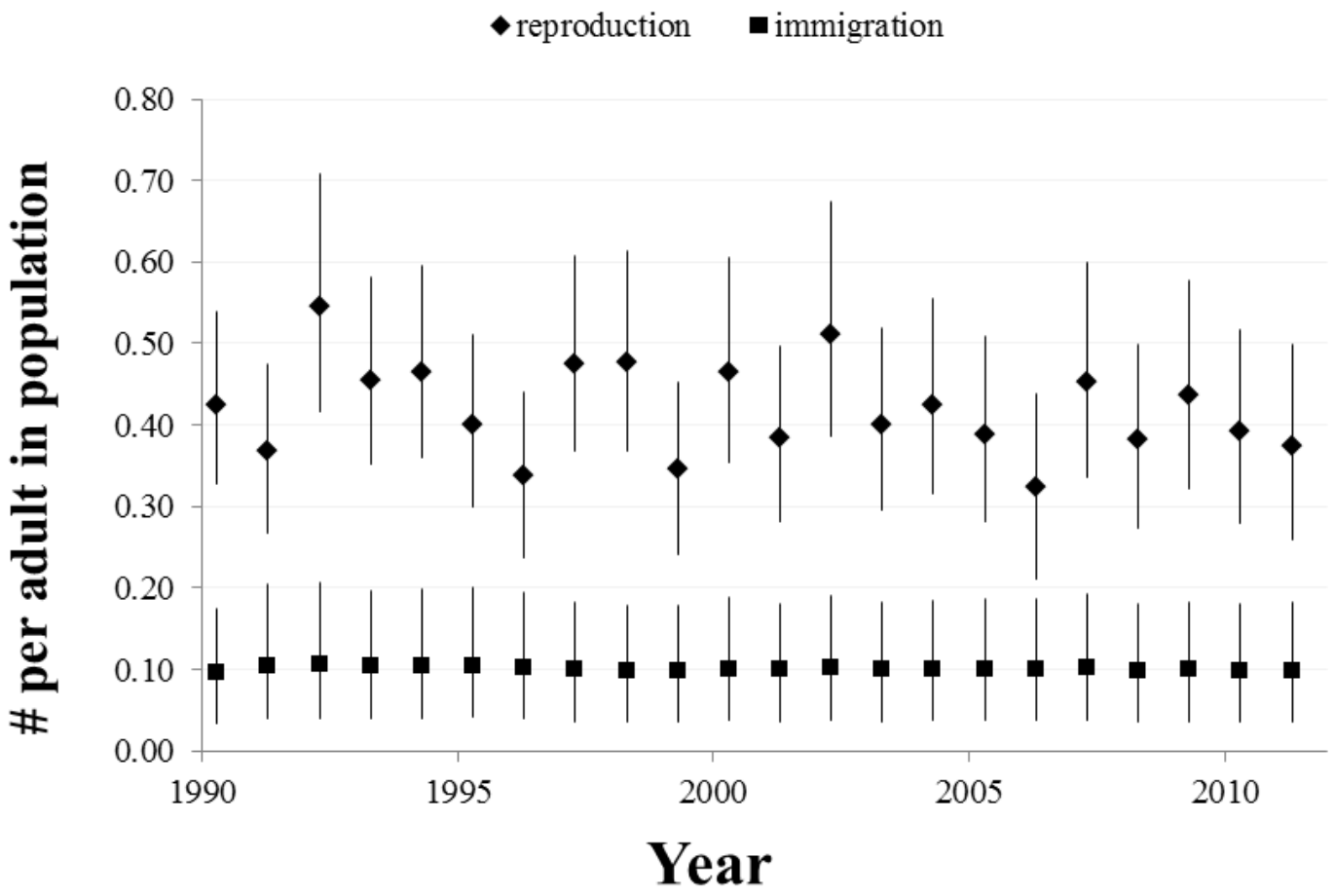

adult
juvenile
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Survival
1990
1995
2000
2005
2010
Year

Figure 2.6. Posterior means of reproductive output (number of young produced per adult) and immigration rate (number of immigrants per adult) from a Bayesian integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990-2011.


reproduction
immigration
per adult in population
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
1990
1995
2000
2005
2010
Year

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APPENDIX 1. Overview of my integrated population model for a California spotted owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1990-2012.

1) Leslie matrix

I used the following Leslie matrix to specify the relationship between population size and demographic rates:

$$\begin{bmatrix} N_{1,\,t+1} \\ N_{2,\,t+1} \end{bmatrix} = \begin{bmatrix} \varphi_{juv}\, f & \varphi_{juv}\, f \\ \varphi_{ad} + imm & \varphi_{ad} + imm \end{bmatrix} \begin{bmatrix} N_{1,\,t} \\ N_{2,\,t} \end{bmatrix}$$

Note that I use "juvenile" to refer to young of the year (i.e., fledglings) and "adult" to refer to birds that are ≥ 1 year of age. The parameters in the matrix were defined as follows:

$N_{1,t}$ = number adults at time t that are 1 year old

$N_{1,t+1}$ = number of adults at time $t + 1$ that are 1 year old

$N_{2,t}$ = number of adults at time t that are ≥ 2 years old

$N_{2,t+1}$ = number of adults at time $t + 1$ that are ≥ 2 years old

φ_{juv} = apparent juvenile survival (i.e., probability of fledglings surviving to 1 year of age)

φ_{ad} = apparent adult survival

f = reproductive output (number of juveniles produced per adult)

imm = immigration rate (number of immigrant adults into the population per adult already in the population)

Thus, the number of 1-year-old adults at time $t + 1$ was:

$$N_{1,t+1} = (N_{1,t} + N_{2,t})\, f_t\, \varphi_{juv,\,t}$$

The number of adults that are ≥ 2 years old at time $t + 1$ was:

$$N_{2,t+1} = (N_{1,t} + N_{2,t})\, (\varphi_{ad,\,t} + imm_t)$$

The total population size of adults at time $t + 1$ was:

$$N_{t+1} = N_{1,t+1} + N_{2,\,t+1}$$

2) Data sources

The three data types used to formulate the individual likelihoods within the IPM framework were population count, reproductive output, and mark-recapture data. I use the following variables to refer to the data:

y = number of adult owls detected each year

J = number of juveniles produced each year

R = number of adults assessed for reproduction each year

m = individual capture histories (both juveniles and adults)

y, J, and R are typically unadjusted counts that do not account for imperfect detection of either adults or juveniles. To obtain improved estimates of these three totals, I used a multi-state occupancy model that characterized the state of each territory and incorporated imperfect detection. Full details of the occupancy model are presented in Chapter 2. *It is important to note that the multi-state occupancy modeling was a separate analytical process that occurred prior to analyzing the IPM.*

The five possible states of a territory were:

0 = no spotted owls present

1 = single adult present

2 = adult pair present, no young produced

3 = adult pair present, one young produced

4 = adult pair present, two young produced

y and J were then calculated from the occupancy status of all territories as:

J = # territories in state 3 + [2 × (# territories in state 4)]

y = # territories in state 1 + [2 × (# territories in states 2, 3, or 4)]

The individual capture histories were obtained directly from the mark-recapture data.

3) Individual likelihoods

I formulated individual likelihoods for each data type, and then multiplied these likelihoods together to obtain a joint likelihood. Estimates for all of the demographic parameters were obtained from this joint likelihood.

Mark-recapture data *(m)*

I summarized the juvenile and adult capture histories as *m*-arrays. I then used a Cormack-Jolly-Seber model to estimate φ_{juv} from the juvenile *m*-array and φ_{ad} from the adult *m*-array. I specified a multinomial distribution for the individual cell probabilities of each array; each cell was a function of φ and *p* (recapture probability).

Reproduction data *(J)*

I specified a Poisson distribution for *J*:

$$J \sim \text{Poisson}\,(R \times f)$$

Count data *(y)*

I used a state-space model to characterize the adult count data. For the state process, there were two components—one for birds that were 1 year old and one for birds that were ≥ 2 years old.

- I specified a Poisson distribution for $N_{1,t+1}$ (the number of 1-year-old adults at time $t + 1$):

  $$N_{1,t+1} \sim \text{Poisson}([N_{1,t} + N_{2,t}]) \times f \times \varphi_{juv,\,t})$$

- I specified the sum of a Poisson-distributed quantity and a binomially distributed quantity for $N_{2,t+1}$ (the number of adults ≥ 2 years old at time t + 1):

  $$N_{2,t+1} \sim \text{Poisson}([N_{1,t} + N_{2,t}]) \times imm_t) + \text{binomial}([N_{1,t} + N_{2,t}]), \varphi_{ad,\,t})$$

For the observation process, I specified a Poisson distribution for *y*:

$$y \sim \text{Poisson}\,(N_{1,t+1} + N_{2,t+1})$$

The complete likelihood for the count data was the product of these three likelihoods (two for the state process, one for the observation process).

Demographic parameters

I specified random time effects for each demographic rate (φ_{juv}, φ_{ad}, *f*, and *imm*). The annual values of each demographic rate ("rate") on the appropriately transformed scale (see below) were realized from normal distributions:

$$\text{"rate"} = \mu + \varepsilon_t$$

where $\mu \sim$ Normal (0, 10000) (i.e., normally distributed with an uninformative prior) and $\varepsilon_t \sim$ Normal (0, σ^2) with σ^2 specified as a uniformly distributed variable with an uninformative prior.

I transformed "rate" using a logit link function for φ_{juv} and φ_{ad}, and using a log link function for *f* and *imm*.

APPENDIX 2. OpenBUGS code for a multi-state occupancy model for a California spotted owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1990-2012.

```
model {

#-------------------------------------------------------------------------------
# Define the parameters and their prior distributions
#-------------------------------------------------------------------------------

# Prior for p1 and initial occupancy

l.p1 ~ dnorm(0,0.0001)I(-10,10)
sig.p1 ~ dunif(0,10)
tau.p1 <- pow(sig.p1,-2)

for (i in 1:5){
Phibeta[i] ~ dgamma(0.1,0.1)
Phi[i] <- Phibeta[i]/sum(Phibeta[])
}

# Induced Dirichlet distribution for detection and transition probabilities with random effects
```

```
for (tt in 1:T){
epsilon.p1[tt] ~ dnorm(0,tau.p1)I(-15,15)
logit(p1[tt]) <- l.p1 + epsilon.p1[tt]

a.p2[tt] ~ dunif(0.5,10)
b.p2[tt] ~ dgamma(1,1)
a.p3E[tt] ~ dunif(0.5,10)
b.p3E[tt] ~ dgamma(1,1)
a.p3L[tt] ~ dunif(0.5,10)
b.p3L[tt] ~ dgamma(1,1)
a.p4E[tt] ~ dunif(0.5,10)
b.p4E[tt] ~ dgamma(1,1)
a.p4L[tt] ~ dunif(0.5,10)
b.p4L[tt] ~ dgamma(1,1)

a.TP1[tt] ~ dunif(0.5,10)
b.TP1[tt] ~ dgamma(1,1)
a.TP2[tt] ~ dunif(0.5,10)
b.TP2[tt] ~ dgamma(1,1)
a.TP3[tt] ~ dunif(0.5,10)
b.TP3[tt] ~ dgamma(1,1)
a.TP4[tt] ~ dunif(0.5,10)
b.TP4[tt] ~ dgamma(1,1)
```

```
a.TP5[tt] ~ dunif(0.5,10)
b.TP5[tt] ~ dgamma(1,1)


      for (i in 1:3){
      p2beta[tt,i] ~ dgamma(a.p2[tt],b.p2[tt])
      p2[tt,i] <- p2beta[tt,i]/sum(p2beta[tt,])
      p3Ebeta[tt,i] ~ dgamma(a.p3E[tt],b.p3E[tt])
      p3E[tt,i] <- p3Ebeta[tt,i]/sum(p3Ebeta[tt,])
      p4Ebeta[tt,i] ~ dgamma(a.p4E[tt],b.p4E[tt])
      p4E[tt,i] <- p4Ebeta[tt,i]/sum(p4Ebeta[tt,])
      }

      for (i in 1:4){
      p3Lbeta[tt,i] ~ dgamma(a.p3L[tt],b.p3L[tt])
      p3L[tt,i] <- p3Lbeta[tt,i]/sum(p3Lbeta[tt,])
      }

      for (i in 1:5){
      TP1beta[tt,i] ~ dgamma(a.TP1[tt],b.TP1[tt])
      TP2beta[tt,i] ~ dgamma(a.TP2[tt],b.TP2[tt])
      TP3beta[tt,i] ~ dgamma(a.TP3[tt],b.TP3[tt])
      TP4beta[tt,i] ~ dgamma(a.TP4[tt],b.TP4[tt])
```

```
      TP5beta[tt,i] ~ dgamma(a.TP5[tt],b.TP5[tt])
      p4Lbeta[tt,i] ~ dgamma(a.p4L[tt],b.p4L[tt])

      TP1[tt,i] <- TP1beta[tt,i]/sum(TP1beta[tt,])
      TP2[tt,i] <- TP2beta[tt,i]/sum(TP2beta[tt,])
      TP3[tt,i] <- TP3beta[tt,i]/sum(TP3beta[tt,])
      TP4[tt,i] <- TP4beta[tt,i]/sum(TP4beta[tt,])
      TP5[tt,i] <- TP5beta[tt,i]/sum(TP5beta[tt,])
      p4L[tt,i] <- p4Lbeta[tt,i]/sum(p4Lbeta[tt,])
      }
}

# Define the transition probabilities for each year

for (tt in 1:T-1) {
      TP[tt,1,1] <- TP1[tt,1]                                    #Pr(transition from 1 to 1)
      TP[tt,1,2] <- TP1[tt,2]                                    #Pr(transition from 1 to 2)
      TP[tt,1,3] <- TP1[tt,3]                                    #Pr(transition from 1 to 3)
      TP[tt,1,4] <- TP1[tt,4]                                    #Pr(transition from 1 to 4)
      TP[tt,1,5] <- TP1[tt,5]                                    #Pr(transition from 1 to 5)

      TP[tt,2,1] <- TP2[tt,1]                                    #Pr(transition from 2 to 1)
      TP[tt,2,2] <- TP2[tt,2]                                    #Pr(transition from 2 to 2)
```

```
    TP[tt,2,3] <- TP2[tt,3]                                    #Pr(transition from 2 to 3)
    TP[tt,2,4] <- TP2[tt,4]                                    #Pr(transition from 2 to 4)
    TP[tt,2,5] <- TP2[tt,5]                                    #Pr(transition from 2 to 5)

    TP[tt,3,1] <- TP3[tt,1]                                    #Pr(transition from 3 to 1)
    TP[tt,3,2] <- TP3[tt,2]                                    #Pr(transition from 3 to 2)
    TP[tt,3,3] <- TP3[tt,3]                                    #Pr(transition from 3 to 3)
    TP[tt,3,4] <- TP3[tt,4]                                    #Pr(transition from 3 to 4)
    TP[tt,3,5] <- TP3[tt,5]                                    #Pr(transition from 3 to 5)

    TP[tt,4,1] <- TP4[tt,1]                                    #Pr(transition from 4 to 1)
    TP[tt,4,2] <- TP4[tt,2]                                    #Pr(transition from 4 to 2)
    TP[tt,4,3] <- TP4[tt,3]                                    #Pr(transition from 4 to 3)
    TP[tt,4,4] <- TP4[tt,4]                                    #Pr(transition from 4 to 4)
    TP[tt,4,5] <- TP4[tt,5]                                    #Pr(transition from 4 to 5)

    TP[tt,5,1] <- TP5[tt,1]                                    #Pr(transition from 5 to 1)
    TP[tt,5,2] <- TP5[tt,2]                                    #Pr(transition from 5 to 2)
    TP[tt,5,3] <- TP5[tt,3]                                    #Pr(transition from 5 to 3)
    TP[tt,5,4] <- TP5[tt,4]                                    #Pr(transition from 5 to 4)
    TP[tt,5,5] <- TP5[tt,5]                                    #Pr(transition from 5 to 5)
}
```

```
# Define the detection probabilities for each year and survey period


for (tt in 1:T) {
     for (jj in 1:k){

     p[tt,1,jj,1] <- p1[tt]                                                    #Pr(observe 1|true state=1)
     p[tt,1,jj,2] <- 0                                                         #Pr(observe 2|true state=1)
     p[tt,1,jj,3] <- 0                                                         #Pr(observe 3|true state=1)
     p[tt,1,jj,4] <- 0                                                         #Pr(observe 4|true state=1)
     p[tt,1,jj,5] <- 1-p1[tt]                                                  #Pr(observe 0|true state=1)

     p[tt,2,jj,1] <- p2[tt,1]                                                  #Pr(observe 1|true state=2)
     p[tt,2,jj,2] <- p2[tt,2]                                                  #Pr(observe 2|true state=2)
     p[tt,2,jj,3] <- 0                                                         #Pr(observe 3|true state=2)
     p[tt,2,jj,4] <- 0                                                         #Pr(observe 4|true state=2)
     p[tt,2,jj,5] <- p2[tt,3]                                                  #Pr(observe 0|true state=2)

     p[tt,3,jj,1] <- E[jj]*p3E[tt,1] + L[jj]*p3L[tt,1]                         #Pr(observe 1|true state=3)
     p[tt,3,jj,2] <- E[jj]*p3E[tt,2] + L[jj]*p3L[tt,2]                         #Pr(observe 2|true state=3)
     p[tt,3,jj,3] <- E[jj]*0 + L[jj]*p3L[tt,3]                                 #Pr(observe 3|true state=3)
     p[tt,3,jj,4] <- 0                                                         #Pr(observe 4|true state=3)
     p[tt,3,jj,5] <- E[jj]*p3E[tt,3] + L[jj]*p3L[tt,4]                         #Pr(observe 0|true state=3)
```

```
     p[tt,4,jj,1] <- E[jj]*p4E[tt,1] + L[jj]*p4L[tt,1]                    #Pr(observe 1|true state=4)
     p[tt,4,jj,2] <- E[jj]*p4E[tt,2] + L[jj]*p4L[tt,2]                    #Pr(observe 2|true state=4)
     p[tt,4,jj,3] <- E[jj]*0 + L[jj]*p4L[tt,3]                            #Pr(observe 3|true state=4)
     p[tt,4,jj,4] <- E[jj]*0 + L[jj]*p4L[tt,4]                            #Pr(observe 4|true state=4)
     p[tt,4,jj,5] <- E[jj]*p4E[tt,3] + L[jj]*p4L[tt,5]                    #Pr(observe 0|true state=4)

     p[tt,5,jj,1] <- 0                                                    #Pr(observe 1|true state=0)
     p[tt,5,jj,2] <- 0                                                    #Pr(observe 2|true state=0)
     p[tt,5,jj,3] <- 0                                                    #Pr(observe 3|true state=0)
     p[tt,5,jj,4] <- 0                                                    #Pr(observe 4|true state=0)
     p[tt,5,jj,5] <- 1                                                    #Pr(observe 0|true state=0)
    }
}

#-------------------------------------------------------------------------------
# Impute the true occupancy state for each territory, each year (Occ[year,territory])
#-------------------------------------------------------------------------------

# s=number of territories
for (ii in 1:s) {
    Occ[1,ii] ~ dcat(Phi[])
```

```
    for (tt in 1:T-1) {
    Occ[tt+1,ii] ~ dcat(TP[tt,Occ[tt,ii], ])
    }

    for (tt in 1:T) {

# Given the imputed occupancy state, what observed state was detected in
# each survey, each year for each territory (Detect[year,territory,survey]).
# Note that 'Detect' is the only data required.

        for (jj in 1:k) {
        Detect[tt,ii,jj] ~ dcat(p[tt,Occ[tt,ii],jj, ])
        }

# Because WinBUGS doesn't have an 'if' function, we need to keep track of
# which of the 5 occupancy states each territory was in each year.
# State[year,state, territory] = 1 if it was in that state that year, and 0 otherwise.

        for (jj in 1:5) {
        State[tt,jj,ii] <- equals(jj,Occ[tt,ii])
        }
    }
}
```

```
#-------------------------------------------------------------------------------

# Estimate means for p and TP

#-------------------------------------------------------------------------------


p1.mean <- sum(p1[1:T])/T

p21.mean <- sum(p2[1:T,1])/T

p22.mean <- sum(p2[1:T,2])/T

p20.mean <- sum(p2[1:T,3])/T

p3E1.mean <- sum(p3E[1:T,1])/T

p3E2.mean <- sum(p3E[1:T,2])/T

p3E0.mean <- sum(p3E[1:T,3])/T

p3L1.mean <- sum(p3L[1:T,1])/T

p3L2.mean <- sum(p3L[1:T,2])/T

p3L3.mean <- sum(p3L[1:T,3])/T

p3L0.mean <- sum(p3L[1:T,4])/T

p4E1.mean <- sum(p4E[1:T,1])/T

p4E2.mean <- sum(p4E[1:T,2])/T

p4E0.mean <- sum(p4E[1:T,3])/T

p4L1.mean <- sum(p4L[1:T,1])/T

p4L2.mean <- sum(p4L[1:T,2])/T

p4L3.mean <- sum(p4L[1:T,3])/T

p4L4.mean <- sum(p4L[1:T,4])/T
```

```
p4L0.mean <- sum(p4L[1:T,5])/T

TP11.mean <- sum(TP1[1:T,1])/T

TP12.mean <- sum(TP1[1:T,2])/T

TP13.mean <- sum(TP1[1:T,3])/T

TP14.mean <- sum(TP1[1:T,4])/T

TP10.mean <- sum(TP1[1:T,5])/T

TP21.mean <- sum(TP2[1:T,1])/T

TP22.mean <- sum(TP2[1:T,2])/T

TP23.mean <- sum(TP2[1:T,3])/T

TP24.mean <- sum(TP2[1:T,4])/T

TP20.mean <- sum(TP2[1:T,5])/T

TP31.mean <- sum(TP3[1:T,1])/T

TP32.mean <- sum(TP3[1:T,2])/T

TP33.mean <- sum(TP3[1:T,3])/T

TP34.mean <- sum(TP3[1:T,4])/T

TP30.mean <- sum(TP3[1:T,5])/T

TP41.mean <- sum(TP4[1:T,1])/T

TP42.mean <- sum(TP4[1:T,2])/T

TP43.mean <- sum(TP4[1:T,3])/T

TP44.mean <- sum(TP4[1:T,4])/T

TP40.mean <- sum(TP4[1:T,5])/T

TP01.mean <- sum(TP5[1:T,1])/T

TP02.mean <- sum(TP5[1:T,2])/T
```

```
TP03.mean <- sum(TP5[1:T,3])/T

TP04.mean <- sum(TP5[1:T,4])/T

TP00.mean <- sum(TP5[1:T,5])/T


#-----------------------------------------------------------------------------------

# Sum up the number of territories in each occupancy state each year

#-----------------------------------------------------------------------------------

for (tt in 1:T) {

     zero[tt] <- sum(State[tt,5,])

     one[tt] <- sum(State[tt,1,])

     two[tt] <- sum(State[tt,2,])

     three[tt] <- sum(State[tt,3,])

     four[tt] <- sum(State[tt,4,])

     popcount[tt] <- one[tt] + 2*(two[tt] + three[tt] + four[tt])

     J[tt] <- three[tt] + 2*(four[tt])

}

}
```

APPENDIX 3. R code for an integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990-2012.

```
# Load data
T <- 2                          # Number of years


# Capture-recapture data: m-array of juveniles and adults (males, females together)
marray.j <- matrix(c(
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,8,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,2,
    0,0,1,0,0,2,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,23,
    0,0,0,0,0,1,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,12,
    0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,16,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,13,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,8,
    0,0,0,0,0,0,0,3,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,15,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,17,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,20,
    0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,4,
    0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,1,0,0,0,0,0,29,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,6,
    0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,2,1,0,0,0,0,11,
```

```
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,2,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,1,0,14,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,9,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,12,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,7,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,3),
    nrow=22,ncol=23,byrow=TRUE)

marray.a <- matrix(c(
    15,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,9,
    0,24,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,5,
    0,0,30,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,5,
    0,0,0,36,1,2,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,8,
    0,0,0,0,26,9,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,12,
    0,0,0,0,0,28,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,10,
    0,0,0,0,0,0,48,1,1,1,0,0,0,0,0,0,0,0,0,0,0,11,
    0,0,0,0,0,0,0,47,3,3,0,0,0,0,0,0,0,0,0,0,0,11,
    0,0,0,0,0,0,0,0,37,3,1,0,0,0,0,0,0,0,0,0,0,14,
    0,0,0,0,0,0,0,0,0,33,3,1,0,0,0,0,0,0,0,0,0,9,
    0,0,0,0,0,0,0,0,0,0,37,0,0,0,0,0,0,1,0,0,0,7,
    0,0,0,0,0,0,0,0,0,0,0,43,1,0,0,0,0,0,0,0,0,4,
    0,0,0,0,0,0,0,0,0,0,0,0,33,2,1,0,1,0,0,0,0,11,
```

```
    0,0,0,0,0,0,0,0,0,0,0,0,0,36,0,0,0,0,0,0,0,0,9,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,32,0,1,0,0,0,0,0,13,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,22,1,0,0,2,0,0,14,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,29,0,0,0,0,0,2,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,32,0,1,0,0,11,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,31,1,0,0,8,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,30,2,0,6,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,28,1,10,
    0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,30,4),
    nrow=22,ncol=23,byrow=TRUE)

# Population count data
popcount <- c(88,75,80,83,82,81,80,81,76,70,67,68,62,65,60,59,55,53,56,50,50,45,42)

# Productivity data
J <- c(38,24,51,40,41,31,21,42,40,19,34,24,37,25,26,21,11,26,19,23,18,14,12)
R <- c(88,75,80,83,82,81,80,81,76,70,67,68,62,65,60,59,55,53,56,50,50,45,42)

# Specify model in BUGS language
sink("ipm.spottedowl1.bug")
cat("
model {
```

```
#------------------------------------------------------------------------
# Integrated Population Model
#  -Age-structured model with 2 age classes:
#       subadults (1 year old) and adults (at least 2 years old)
#  -Breeding census (April-August)
#  -All vital rates are time-dependent (random)
#  -Explicit estimate of immigration
#------------------------------------------------------------------------


#------------------------------------------------------------------------
# 1. Define the priors for the parameters
#------------------------------------------------------------------------


# Initial population sizes
N1[1] ~ dnorm(100,0.0001)I(0,)                                  # 1-year old subadults
NadSurv[1] ~ dnorm(100,0.0001)I(0,)                             # Adults >= 2 years old
Nadimm[1] ~ dnorm(100,0.0001)I(0,)                              # Immigrants


# Mean demographic parameters (on appropriate scale)
l.mphij ~ dnorm(0,0.0001)I(-10,10)                              # Bounded to help with convergence
l.mphia ~ dnorm(0,0.0001)I(-10,10)
l.mfec ~ dnorm(0,0.0001)I(-10,10)
l.mimm ~ dnorm(0,0.0001)I(-10,10)
```

```
l.p ~ dnorm(0,0.0001)I(-10,10)


# Precision of standard deviations of temporal variability
sig.phij ~ dunif(0,10)
tau.phij <- pow(sig.phij,-2)
sig.phia ~ dunif(0,10)
tau.phia <- pow(sig.phia,-2)
sig.fec ~ dunif(0,10)
tau.fec <- pow(sig.fec,-2)
sig.imm ~ dunif(0,10)
tau.imm <- pow(sig.imm,-2)
sig.p ~ dunif(0,10)
tau.p <- pow(sig.p,-2)

# Distribution of error terms (bounded to help with convergence)
for (t in 1:(T-1)){
    epsilon.phij[t] ~ dnorm(0,tau.phij)I(-15,15)
    epsilon.phia[t] ~ dnorm(0,tau.phia)I(-15,15)
    epsilon.fec[t] ~ dnorm(0,tau.fec)I(-15,15)
    epsilon.imm[t] ~ dnorm(0,tau.imm)I(-15,15)
    epsilon.p[t] ~ dnorm(0,tau.p)I(-15,15)
}
```

```
#------------------------------------------------------------------
# 2. Constrain the parameters
#------------------------------------------------------------------

for (t in 1:(T-1)){
    logit(phij[t]) <- l.mphij+epsilon.phij[t]                    # Apparent juvenile survival
    logit(phia[t]) <- l.mphia+epsilon.phia[t]
# Apparent adult survival
    log(f[t]) <- l.mfec+epsilon.fec[t]                           # Productivity
    log(omega[t]) <- l.mimm+epsilon.imm[t]                       # Immigration
    logit(p[t]) <- l.p+epsilon.p[t]                              # Recapture probability
}

#------------------------------------------------------------------
# 3. Derived parameters
#------------------------------------------------------------------

mphij <- exp(l.mphij)/(1+exp(l.mphij))                           # Mean juvenile survival probability
mphia <- exp(l.mphia)/(1+exp(l.mphia))                           # Mean adult survival probability
mfec <- exp(l.mfec)                                              # Mean productivity
mimm <- exp(l.mimm)                                              # Mean immigration rate
mp <- exp(l.p)/(1+exp(l.p))                                      # Mean immigration rate
```

```
# Population growth rate, realized population change (RPC)

RPC[1] <- 1
for (t in 1:(T-1)){
    lambda[t] <- Ntot[t+1]/Ntot[t]
    loglam[t] <- log(lambda[t])
    RPC[t+1] <- RPC[t]*lambda[t]
    RPC.pop[t+1] <- Ntot[t+1]/Ntot[1]
}
mlam <- exp((1/(T-1))*sum(loglam[1:(T-1)]))                    # Geometric mean of lambda


#------------------------------------------------------------------------
# 4. The likelihoods of the individual data sets
#------------------------------------------------------------------------

# 4.1. Likelihood for population count data (state-space model)

    # 4.1.1. System process
    for (t in 2:T){
              mean1[t] <- f[t-1]*phij[t-1]*Ntot[t-1]
              N1[t] ~ dpois(mean1[t])
```

```
            NadSurv[t] ~ dbin(phia[t-1],Ntot[t-1])
            mpo[t] <- Ntot[t-1]*omega[t-1]
            Nadimm[t] ~ dpois(mpo[t])
    }

    # 4.1.2. Observation process
    for (t in 1:T){
             Ntot[t] <- NadSurv[t]+Nadimm[t]+N1[t]
             y[t] ~ dpois(Ntot[t])
    }

# 4.2. Likelihood for capture-recapture data: CJS model (2 age classes)

# Multinomial likelihood
for (t in 1:(T-1)){
    marray.j[t,1:T] ~ dmulti(pr.j[t,],r.j[t])
    marray.a[t,1:T] ~ dmulti(pr.a[t,],r.a[t])
}

# Calculate number of released individuals
for (t in 1:(T-1)){
    r.j[t] <- sum(marray.j[t,])
    r.a[t] <- sum(marray.a[t,])
```

```
}


# m-array cell probabilities for juveniles
for (t in 1:(T-1)){
    q[t] <- 1-p[t]


    # Main diagonal
    pr.j[t,t] <- phij[t]*p[t]


    # Above main diagonal
    for (j in (t+1):(T-1)){
             pr.j[t,j] <- phij[t]*prod(phia[(t+1):j])*prod(q[t:(j-1)])*p[j]
    }  # j


    # Below main diagonal
    for (j in 1:(t-1)){
                                                                          pr.j[t,j] <- 0
    }  # j


    # Last columnn
    pr.j[t,T] <- 1-sum(pr.j[t,1:(T-1)])
}  # t
```

```
# m-array cell probabilities for adults
for (t in 1:(T-1)){

    # Main diagonal
    pr.a[t,t] <- phia[t]*p[t]

    # Above main diagonal
    for (j in (t+1):(T-1)){
              pr.a[t,j] <- prod(phia[t:j])*prod(q[t:(j-1)])*p[j]
    }  # j

    # Below main diagonal
    for (j in 1:(t-1)){
              pr.a[t,j] <- 0
    }  # j

    # Last columnn
    pr.a[t,T] <- 1-sum(pr.a[t,1:(T-1)])
}  # t

# 4.3. Likelihood for productivity data: Poisson regression
for (t in 1:(T-1)){
    rho[t] <- R[t]*f[t]
```

```
    J[t] ~ dpois(rho[t])
}
}
",fill=TRUE)
sink()

library(R2WinBUGS)

# Specify location of WinBUGS program
bugs.dir <- "C:/Program Files (x86)/WinBUGS14/"

# Bundle data
bugs.data <- list(T=T,marray.j=marray.j,marray.a=marray.a,y=popcount,J=J,R=R)

# Initial values
inits <- function(){list(l.mphij=rnorm(1,0.2,0.5),l.mphia=rnorm(1,0.2,0.5),l.mfec=rnorm(1,0.2,0.5),
    l.mimm=rnorm(1,0.2,0.5),l.p=rnorm(1,0.2,1),sig.phij=runif(1,0.1,10),sig.phia=runif(1,0.1,10),
    sig.fec=runif(1,0.1,10),sig.imm=runif(1,0.1,10),N1=round(runif(T,1,50),0),
    NadSurv=round(runif(T,80,100),0),Nadimm=round(runif(T,1,50),0))}

# Parameters monitored
parameters <- c("phij","phia","f","omega","p","mphij","mphia","mfec","mimm","mp","sig.phij",
    "sig.phia","sig.fec","sig.imm","sig.p","N1","NadSurv","Nadimm","Ntot","lambda","mlam","RPC","RPC.pop")
```

```
# MCMC settings

ni <- 60000

nt <- 1

nb <- 10000

nc <- 3


# Call WinBUGS from R

ipm.spottedowl2 <- bugs(bugs.data,inits,parameters,"ipm.spottedowl1.bug",n.chains=nc,n.thin=nt,

    n.iter=ni,n.burnin=nb,debug=TRUE,bugs.directory=bugs.dir,working.directory=getwd())
```